THE INFLUENCE OF CLIMATE AND VEGETATION ON THE WATER BALANCE OF MONTANE AND ALPINE ECOSYSTEMS

INAUGURAL DISSERTATION

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Dekan

Whence comes all the motive power? What is the spring that drives all? We see the ocean rise and fall, the rivers flow, the wind, rain, hail, and snow beat on our windows, the trains and steamers come and go; we hear the rattling noise of carriages, the voices from the street; we feel, smell, and taste; and we think of all this. And all this movement, from the surging of the mighty ocean to that subtle movement concerned in our thought, has but one common cause. All this energy emanates from one single center, one single source - the sun. The sun is the spring that drives all. The sun maintains all human life and supplies all human energy.

Nikola Tesla (1856 - 1943)

Source: Tesla N 1900: The Problem of Increasing Human Energy: With Special Reference to the Harnessing of the Sun's Energy.
Century Illustrated Magazine: 175-211

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Chapter 1: General introduction

The influence of climate and vegetation on the water balance of montane and alpine ecosystems

The total short- and longwave incoming solar radiation, the global radiation G, minus the reflectance from the ground or vegetation (albedo), yields net radiation (Q). Over terrestrial surfaces, the energy contained in Q is partitioned into evaporation from land and vegetation (latent energy: L), warming of the air (sensible heat: H) and warming of the soil (soil heat flux h; Equation 1).

$$Q = H + L + h \qquad \text{Eq. 1}$$

The energy consumed by thermal radiation (black body radiation) is negligible during the day (but matters during clear nights), soil heat flux is also a small fraction and close to zero over 24 hours, and the biochemical energy fixed by photosynthesis is so small either that equation 1 becomes reduced to 3 terms, with the ratio between H and L, the Bowen ratio, determining the local heat balance.

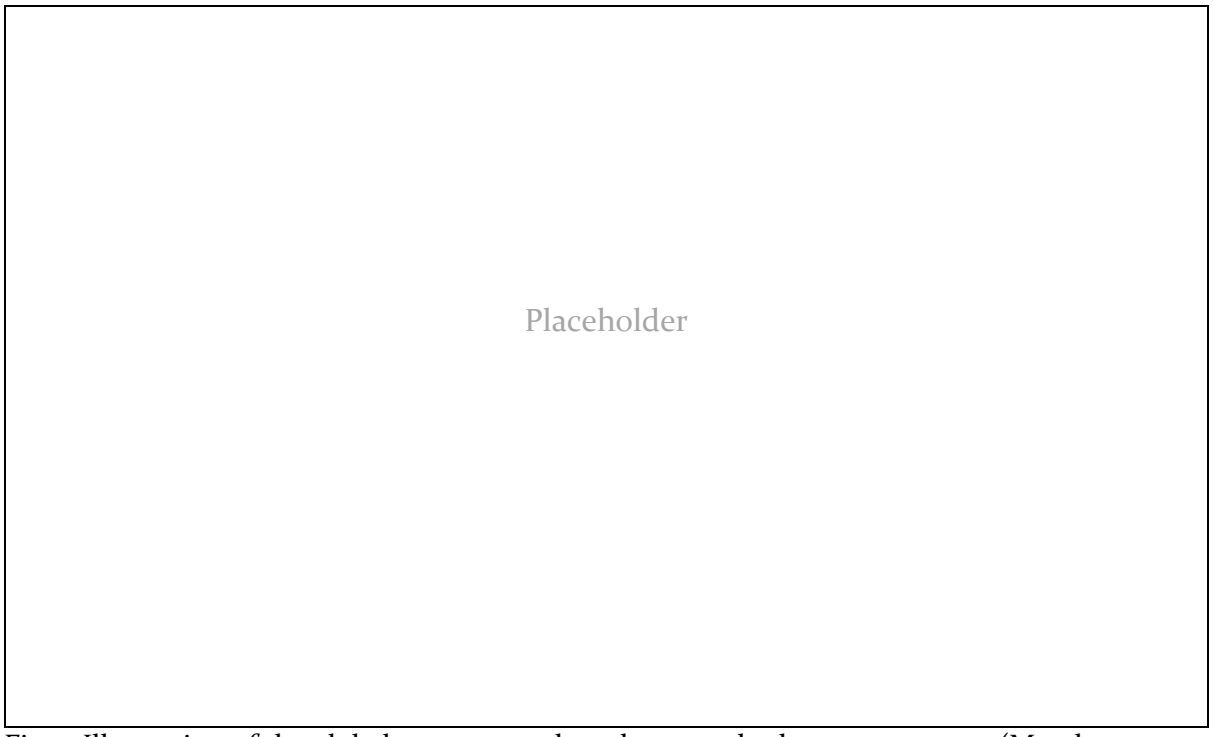

Fig. 1. Illustration of the global mean annual earth energy budget components (March 2000 – May 2004) in W m^{-2}. The size of the arrows indicates the magnitude of these fluxes (from Trenberth *et al.*, 1997).

The latent heat flux, that is evapotranspiration (ET), is one of the key components of the ecosystem water balance equation (Eq. 2, Fig. 2) and can be written as follows:

$$P = R + ET + \Delta S \qquad \text{Eq. 2}$$

The amount of precipitation (P) equals the sum of runoff or deep seepage (R), evapotranspiration (ET) and the difference in stored soil moisture (ΔS; Equation 2). ET is composed of evaporation from the soil (E) and transpiration by the vegetation (T). ET also includes evaporation of precipitation that is intercepted by the vegetation (I) and evaporated back to the atmosphere without adding to soil moisture or runoff. Over longer periods, for instance a whole year, ΔS equals zero. Soil moisture influences ET but also plant growth and nutrient cycling. The relative magnitude of precipitation and ET determines catchment discharge and with this, the amount of water available for human usage, for example for urban supplies, irrigation and the generation of hydro-power.

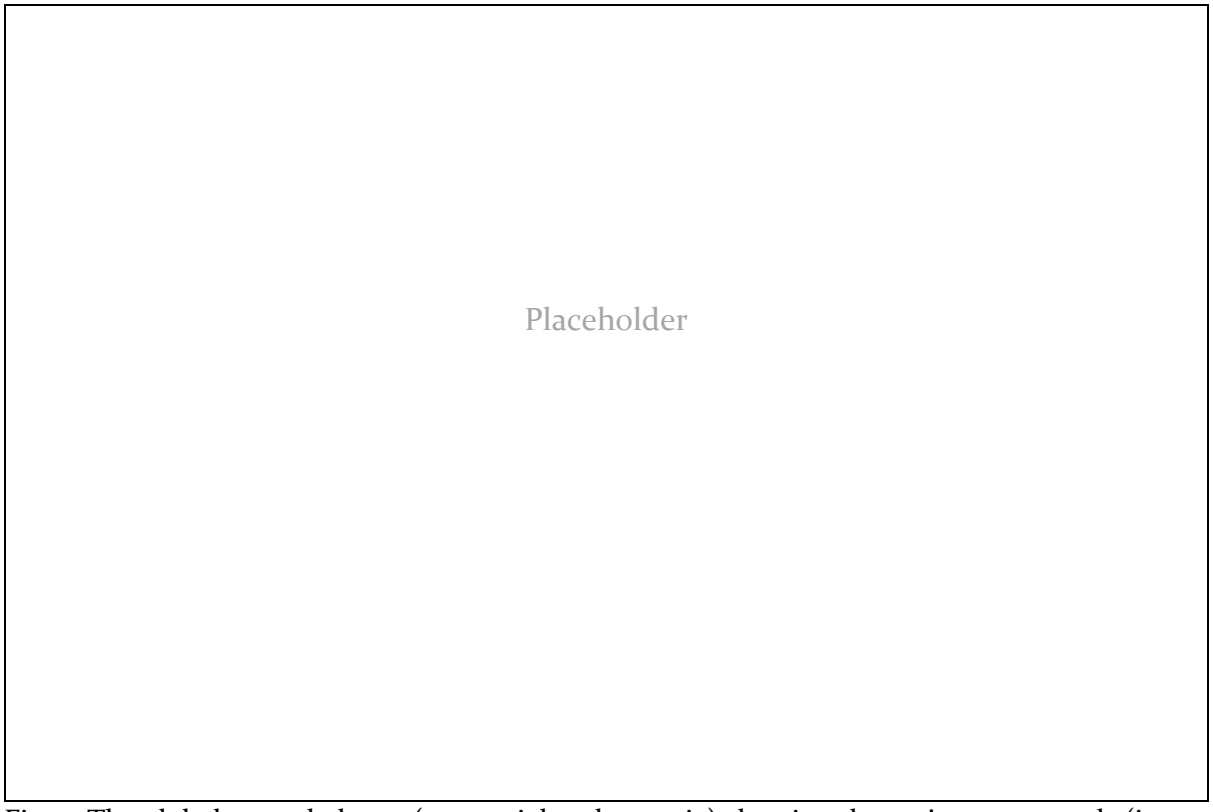

Fig. 2. The global water balance (terrestrial and oceanic) showing the major water pools (in boxes) and fluxes (arrows; compiled from different sources in Oki and Kanae, 2006). Arrows indicate fluxes in 1000 $km^3\ a^{-1}$, boxes inidcate the magnitude of the pools in 1000 km^3, within parentheses the surface area of the major land cover types is given in million km^2.

Globally, ET consumes slightly more than half of the available solar energy (net radiation; Trenberth *et al.*, 2009). ET is determined by weather conditions and land cover (Allen *et al.*, 1998) and makes up 60% of the terrestrial water cycle (Oki and Kanae, 2006,Fig. 2). Plant transpiration is the main component (70%) of ET (Jasechko *et al.*, 2013), also for alpine plant communities (Körner, 2003). While climatic factors (evaporative forcing) jointly determine the potential depth of ET (when no restrictions of water availability come into play), vegetation (1) couples the rooted soil volume to the atmosphere, (2) commonly increases the evaporating surface by its foliage (leaf area index, LAI), and (3) mediates evaporative forcing by regulating T with its stomates. Hence, ET commonly exceeds evaporation from a free water surface. With their periodic water storage, soils represent a buffer between supply (P) and demand (ET).

So, ET is driven by climatic and vegetation factors, with the latter often shaped by land use practices such as deforestation, grazing or mowing, but also by land abandonment, shrub encroachment and reforestation. The influence of such man-made vegetation changes on the ecosystem water balance in mountain terrain is the topic of this thesis. High elevation land cover currently undergoes rapid changes in many parts of the worlds. These changes go from overexploitation and destruction causing erosion problems in developing countries (Hurni 1988; Braimoh and Vlek, 2008) to land abandonment that leads to tall grass swards, shrub establishment and eventually often, the return of the montane forest in developed countries such as in the Alps (Niedrist *et al.*, 2009; Inauen *et al.,* 2013).

In most parts of the Alps, precipitation by far exceeds ET and hence, montane and alpine catchments discharge a lot of water to the European lowlands (Viviroli and Weingartner, 2004; Viviroli *et al.*, 2007), with a great potential for hydroelectric power production. In Switzerland, 56% of the electricity is generated from hydropower plants

(Swiss Federal Office for Energy, 2016). In mountainous landscapes, climate and vegetation exhibit large spatial variation and ET has been shown to vary significantly across montane and alpine plant communities (Körner *et al.*, 1989; Inauen *et al.,* 2013). These differences in ET depend on the biomass and height of vegetation, particularly the transpiring plant biomass or LAI (Van den Bergh *et al.*, 2013; Obojes *et al.*, 2014) and climate (Van den Bergh *et al.*, 2013). This strong local variation of the drivers of ET makes it very difficult to predict ET at landscape scale. ET is positively associated with leaf area up to values of around 3 $m^2 m^{-2}$. Due to the saturation of the canopy conductance for water vapour transfer, ET generally does not increase further when leaf area index exceeds these levels (Schulze *et al.*, 1994; Hammerle *et al.*, 2008). Hence, if grazing or mowing reduces LAI below that saturation level, it can significantly affect the water balance.

In my thesis, I aim at quantifying the effects of different land cover types and climatic conditions on ET, and with this, on the hydrology of mountain watersheds. Focus was on effects of land use on grass- and shrubland ET and how these effects change with elevation. In the following, the three main chapters of the thesis will be introduced in more detail. Within the second chapter I will elaborate on the interactions between climate and vegetation (biomass and heigth) and how these contribute to ET rates along an elevational gradient. The third and fourth chapter address more applied questions, exploring the effects of current changes in land use on ET, and with this, the water balance. These chapters close with estimates of the effects of land use on the hydro-electric potential of a high elevation catchment (the upper Reuss catchment in the Swiss central Alps; the Ursern valley).

Chapter 2 explores the relative significance of the change in climate and vegetation with increasing elevation. With increasing elevation, air temperature declines. Because cold air can carry less humidity, the vapour pressure deficit commonly also decreases (McVicar *et al.*, 2007). Atmospheric pressure decreases by about 10 kPa km^{-1} (Burman *et al.*, 1987; Körner 2003) causing the diffusivity of water vapour to rise. The net effect

of these physical changes with elevation is unclear. The decrease of air temperature is about 6 K km^{-1} with some seasonal and strong regional variation (Dodson and Marks, 1997; Rolland, 2003; McVicar *et al.*, 2007). Up to about 3000 m a.s.l., during summer time, shortwave solar radiation in the Alps is rather independent of elevation (Marty *et al.*, 2002), because the increase of clear sky radiation with altitude (due to reduced turbidity) is compensated by altitudinally increasing cloudiness. In addition, the snow free period becomes shorter with elevation.

Grasslands cover some 40% of the global land surface (both intensively and extensively managed; White *et al.*, 2000) and are a major land cover type in the European Alps. Due to the elevational decline in air temperatures and a shortening of the growing season, both biomass and LAI decrease with elevation (Cernusca and Seeber, 1981; Körner 2003). When LAI levels drop below ca. 3 m^2 m^{-2}, ET would be expected to decrease (see above). However, at alpine sites, the short and often very dense vegetation canopy causes solar heat accumulation (high aerodynamic resistance to heat convection), resulting in steeper leaf to air temperature differences which enhance ET (Smith and Geller, 1979). These canopy warming effects are much less pronounced in the taller grassland at lower elevations. So, low stature alpine plants become increasingly decoupled from free atmospheric circulation (Cernusca and Seeber, 1981; Körner and Cochrane, 1983). In Chapter 2 of my thesis, I aim at deciphering the causes of observed elevational trends in ET by comparing measured ET of the local vegetation with evaporation from an evaporimeter (atmometer) and by applying a meteorological model (Penman-Monteith model for ET).

In order to determine how climate and vegetation contribute to the elevational trends in ET, I set up an experiment that permits to quantify (a) climatic forcing (here termed atmospheric evaporative demand, AED, by employing evaporimeters), (b) the rates of ET and the associated biomass for of a range of native grassland types, as well as (c) climatic conditions. The elevation gradient in the upper Reuss catchment (Ursern valley, central Swiss Alps) included three sites, at 1490 (low: L), 1960 (mid: M) and

2440 m a.s.l. (high: H). Changes in ET with elevation different from those in AED should reflect influences from vegetation. This chapter thus explains whether ET from montane to alpine grasslands is governed predominantly by climate or vegetation traits (biomass, LAI) or a combination of both.

Throughout human history the intensity and extent of land use has shaped our natural surroundings (Matthews, 1983; Houghton, 1994; DeFries *et al.*, 2004). This has affected land cover, ecosystem processes (Vitousek, 1994; Vitousek *et al.*, 1997; Guo and Gifford, 2002; Foley *et al.,* 2005) and climate (Shukla and Mintz, 1982; Stohlgren *et al.*, 1998; Pielke *et al.*, 2002). Effects of land use on the water balance have been estimated to exceed those related to increases in atmospheric CO_2 and climate change (Piao *et al.*, 2007; Inauen *et al.*, 2013). As a result of increasing land use, forests, woodlands and natural grasslands have been replaced by arable lands, hay fields and pastures (Matthews, 1983). In grasslands, the intensity of mowing and grazing influences leaf area and with it potentially also ET.

During the second half of the last century however, this trend of land use intensification has been reversed in many parts of the world (Houghton *et al.*, 1999). As a consequence, shrublands have expanded worldwide (Archer *et al.*, 1995; Roques *et al.*, 2001). Also the Alps have a long history of land use (Bätzing, 2015). Here, recent socio-economic changes have led to a decline in the number of farms, abandonment of high (low yielding) lands and conversely, intensification of agricultural use on low, easily accessible and fertile grounds (Rudel *et al.*, 2005; Rudmann-Maurer *et al.,* 2008). The less accessible (steep) and less productive lands have become abandoned (particularly at high montane and alpine elevations; MacDonald *et al.*, 2000; Tasser *et al.*, 2005; Gellrich *et al.*, 2007; Niedrist *et al.,* 2009). Abandonment has led to the development of tall grass swards with high leaf area and the accumulation of plant litter and necromass (Tappeiner and Cernusca 1989; Wohlfahrt *et al.,* 2003). Above the potential tree line, grassland abandonment commonly leads to the establishment of dwarf shrub communities (Tasser and Tappeiner, 2002). On steep and rather moist

slopes, abandoned montane grasslands are often colonised by various species of tall shrubs of which *Alnus viridis* is the most aggressive one (Anthelme *et al.*, 2003; Anthelme *et al.*, 2007; Bühlmann *et al.,* 2014). Between 1912 and 1997, 34% of all pastures have been abandoned in Switzerland (Bauer *et al.*, 2007) and the cover by green alder has doubled in some regions of the Swiss Alps (Huber and Frehner, 2012). Moderate grazing creates opportunities for rare species that would otherwise be suppressed (Körner *et al.*, 2006). The cessation of grazing has hence led to a reduction in biodiversity (Anthelme *et al.*, 2001; Tasser and Tappeiner, 2002; Anthelme *et al.*, 2003; Anthelme *et al.*, 2007).

The vigour of *Alnus viridis* can be explained by its symbiotic fixation of atmospheric di-nitrogen (N_2). The resulting high nitrate availability creates a very lush understorey. This is an environment in which small seeded montane forest tree species have difficulties to establish. Thus, the encroachment by *Alnus viridis* into former pastures has also inhibited the succession towards the natural montane forest (Tappeiner and Cernusca, 1993; Hiltbrunner *et al.,* 2014). Only centuries after *Alnus* expansion conifer trees may slowly take over (Bühlmann *et al.,* 2014).

Abandonment has strong effects on ecosystem functioning. Often, soil C and N pools increase (Post and Kwon, 2000; Thuille *et al.*, 2000; Hooker and Compton, 2003). For montane grasslands however, expansion of *Alnus viridis* was shown to reduce the ecosystem carbon and the soil nitrogen pools (Bühlmann *et al.*, 2016). Also the water balance is most likely to be affected. Shrubland or forest establishment has often been shown to increase ET and therefore to reduce runoff (Bosch and Hewlett, 1982; Lorup *et al.*, 1998; Brown *et al.*, 2005; Farley *et al.*, 2005 Dumas 2011). It has been estimated that worldwide, ET was reduced by 3.000 $km^3\ a^{-1}$ (ca. -4%) due to deforestation (Gordon *et al.*, 2005; Fig. 2).

Chapter 3 explores these questions for the early stages where abandonment has led to tall swards and colonisation by dwarf shrub communities. Earlier attempts at quantifying the hydrological impact of abandonment on alpine grasslands have shown that ET increases by about 10% (Körner and Nakhutsrishvili, 1986; Körner *et al.,* 1989; Tappeiner and Cernusca, 1998). However, effects can be much larger for more vigorous alpine grassland types (Inauen *et al.,* 2013). Because land use removes more biomass at montane elevations, I expect stronger increases in ET due to abandonment at the lower part of the elevational gradient. When it comes to the hydro-electric potential of the catchment I expect that these higher ET rates of tall swards at montane elevation are levelled off by lower falling height of water (lower kinetic energy). Also the montane land area is relatively small (as it is the case in the test catchment Upper Reuss valley). In contrast, the smaller effect of land use or abandonment om ET at high elevation should become enhanced by a greater falling height (potential energy) and scales to larger effects for the entire catchment because of the much larger land area fraction.

To test the effect of grazing on the water balance, a manipulative experiment was set-up. ET rates for bright days were measured using weighable lysimeters fitted with grassland monoliths (WLs). To measure ET for the entire growing season I solved the water balance equation for monoliths in deep seepage collectors (DSCs), using on-site precipitation data and deep seepage amounts. Half of these vegetation units were clipped to simulate grazing. I also used monoliths with *Calluna vulgaris* and *Vaccinium myrtillus* to explore the hydrological consequences of dwarf shrub expansion at L and M. At H, besides the most typical alpine grassland types with *Carex curvula* and *Nardus stricta*, the set-up included monoliths with *Agrostis schraderiana* and *Deschampsia flexuosa* to quantify the effects of the establishment of particularly tall grass swards at this highest elevation. *Nardus stricta* swards were included at all three elevations because this grassland type occurs across the entire elevational gradient.

In **Chapter 4**, I explore the hydrological effects of encroachment of former pastures by the native, tall shrub *Alnus viridis* in comparison to adjacent, commonly grazed pastures I combined data from WLs (pastures and *Alnus* understorey) and sap flow data for *Alnus* stems based on the energy balance method. These measurements were conducted at a montane site where the *Alnus* cover has strongly increased during the last five decades. Using weather parameters recorded at the test site, ET measurements from pastures and *Alnus* shrubland were extrapolated to the growing season. In order to estimate the economic effect of the resulting runoff reduction compared to pastures, the extra ET (= reduced runoff) was converted to the corresponding monetary value of continued landscape care. Such costs should be accounted for in land use policies.

Objectives / hypotheses

1) Bright day ET is expected not to change with elevation because the reduced atmospheric demand should be compensated for by a steeper leaf to air vapour pressure gradient (canopy heating).
2) Because land use removes more biomass at montane compared to alpine sites, I expect more significant land use effects at montane elevations.
3) Large abandonment effects at montane sites translate into relatively small effects on the hydro-electric potential as falling height (kinetic energy) is limited and because the montane area in our model catchment is small compared to the high montane and alpine belts.
4) *Alnus* expansion is expected to not enhance ET as effects of stronger aerodynamic coupling in *Alnus* should be offset by lower surface temperatures. Thus, differences in ET compared to pastures should be particularly pronounced during days with strong atmospheric forcing (high wind speed, high VPD).

Chapter 2 is published: Van den Bergh T, Inauen N, Hiltbrunner E, Körner C 2013. Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps. Journal of Hydrology, 500: 75-83.

Chapter 3 needs to be submitted

Chapter 4 is published: van den Bergh T, Körner C, Hiltbrunner E 2017. Alnus shrub expansion increases evapotranspiration in the Swiss Alps. Regional Environmental Change, 18: 1–11.

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Chapter 2

Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps

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Abstract

Atmospheric conditions and plant cover are the two main determinants of evapotranspiration (ET), and both strongly depend on elevation. The objective of this work was to separate the two effects across a 1 km elevation gradient and compare theoretical and experimental approaches in order to improve hydrological models for mountainous regions. We used the Penman-Monteith model (FAO-56 procedure) and atmometers (evaporimeters) in combination with grassland weighable lysimeters (WL) and deep seepage collectors (DSC) positioned at three sites at 1490, 1960 and 2440 m of elevation (referred to as low, mid and high: L, M and H) in the Swiss Alps to quantify climatic and vegetation effects on ET. Atmometers and the Penman-Monteith model were used to quantify atmospheric evaporative demand and WLs were employed to measure ET during clear days (WLET). DSCs were used to calculate ET rates from the water balance equation over longer time periods (DSCET) during summer in 2010 and 2011. During clear days, Penman-Monteith evapotranspiration (PMET) was reduced by 11% at the high site in comparison to the low site, atmometer evaporation (AE) was reduced by 23%, and daytime WLET rates decreased by 37%. Over longer time spans (close to three months), PMET decreased by an average of 10% (14% and 6% for 2010 and 2011) along the entire elevational gradient, and DSCET dropped by a mean of 35% (45% and 25% during 2010 and 2011). The steeper elevational gradient in DSCET in 2010 was probably caused by the early onset of the growing season at low elevation during that year. Reductions in WLET and DSCET with elevation were thus consistently larger than the decline in both AE and PMET. Lower vascular plant biomass at high elevation causes a reduction in ET that is approximately as large as the reduction in ET by reduced atmospheric forcing. These findings call for a revision of the view that evapotranspiration, during the growing season, is explained by season length only (assuming no effect of elevation on a daily basis). Hydrological models in high elevation catchments needs to account for elevational changes in plant cover (amount of transpiring biomass, LAI), even within the same type of land cover as shown here for grassland.

Keywords

atmometer; grassland; hydrology; lysimeter; mountain; Penman-Monteith equation

Introduction

One classical question that has long occupied meteorologists and hydrologists concerns the way evapotranspiration (ET) is related to elevation. Meteorologists have focussed on effects of elevational shifts in atmospheric conditions on evaporation rates (*e.g.* the early works by HB de Saussure, see Barry, 1978), while hydrologists employed the water balance equation to calculate ET for catchments from different elevations from precipitation and runoff (*e.g.* Menzel and Lang, 1998). Yet, ET rates are inherently tied to both climatic conditions and land surface properties, both of which are affected by elevation in different ways. Hydrological models for mountain regions often describe vegetation induced variability in ET by using coarse land cover categories such as forest, grassland, permanent snow, etc. (*e.g.* Gurtz *et al.,* 1999). Grassland is a major vegetation type in montane and alpine catchments (Körner, 2009; Tappeiner *et al.,* 2008) and within this vegetation type, transpiring leaf mass and vegetation height vary considerably with elevation. This study aims to quantify the separate contributions of vegetation and climatic forcing to growing season ET. In the following, we use the term elevation for land surface properties and the surface boundary layer, and the term altitude for conditions in the free atmosphere (McVicar and Körner, 2012).

Climatic conditions change markedly with elevation. Some of those changes are common altitude related phenomena such as the decline in atmospheric pressure and air temperature. Other climatic factors such as cloudiness, wind speed, and precipitation show strong regional variation and are not related to altitude in a systematic manner (Barry, 1981; Körner, 2003; Körner, 2007). In the European Alps, precipitation increases with increasing altitude (Frei and Schär, 1998). Worldwide however, the effect of altitude on precipitation has been shown to depend on latitude (see Lauscher's review, 1976; Körner, 2007). Atmospheric pressure decreases by about 10 kPa km^{-1} (for altitudes up to 4 km; Burman *et al.,* 1987), which causes air temperatures to decline. Generally, for mid latitude mountain ranges, annual air temperature lapse rates are smaller than summer time temperature lapse rates which

average about 6.0 K km^{-1} in the central Alps (Dodson and Marks, 1997; McVicar *et al.,* 2007; Rolland, 2003; Tabony, 1985).

From the Chapman-Enskog equation it can be deduced that the diffusion coefficient of water in air is inversely proportional to atmospheric pressure, while at the same time, it shows a positive power relationship with air temperature (Reid *et al.,* 1987). This means that a reduction in air pressure leads to an increase in the diffusivity of water vapour in air (and thus enhances transpiration), while a reduction in air temperature alone has the opposite (but smaller) effect. As a result of declining air temperature, the vapour pressure deficit of the atmosphere decreases with altitude (McVicar *et al.,* 2007). This lower vapour pressure deficit (VPD) should reduce evaporation rates. Under clear sky conditions, net solar radiation (the balance between incoming and outgoing solar radiation), has been reported to be independent of elevation during summer (Marty *et al.,* 2002).

Grassland is affected by elevation in a number of ways. While leaf area per unit of land area (LAI) and leaf biomass decrease with elevation, standing necromass often increases (Cernusca and Seeber, 1981). Although these increasing amounts of dead plant material do not transpire, they increase interception of rainfall and add to the aerodynamic resistance of the canopy (Cernusca and Seeber, 1981). Further, leaf to air temperature differences are larger at high elevations compared to low elevations because low stature vegetation is less coupled to the atmosphere (Cernusca and Seeber, 1981; Körner and Cochrane, 1983). Higher surface to atmosphere temperature differences result in steeper leaf to air water vapour concentration gradients and can be expected to enhance transpiration (Smith and Geller, 1979). Stomatal density and leaf diffusive conductance increase with elevation (Körner and Mayr, 1981; Körner, 2003) and can potentially compensate for the effect of reduced LAI at high elevation. However, the net effect of higher stomatal conductance at high elevation cannot be fully resolved since stomatal, aerodynamic and topography induced resistances to vapour diffusion all act in series. Owing to these complex interactions between

atmospheric conditions and vegetation, it is not *a priori* clear how evapotranspiration rates are affected by elevation.

A decrease in atmospheric pressure has been shown to lead to higher rates of pan evaporation (Rohwer, 1931). Decreases in air temperature and VPD however, more than offset this effect and cause evaporation rates from a free water surface to decline with elevation (Blaney, 1958; Longacre and Blaney, 1962 and references therein; Shaw, 1909; Young, 1947). This is supported by theoretical studies (see Gale, 1972; Smith and Geller, 1979). Evaporation may however, increase with elevation due to temperature inversion (*e.g.* Nullet and Juvik, 1994). Finally, exposure, through effects on intercepted solar radiation and on wind speed exerts additional effects (Peck and Pfankuch, 1963; Peck, 1967). At annual time scales, ET rates decrease with elevation (Lang, 1981) because the length of the snow free period decreases with elevation in high latitude mountains (Körner *et al.,* 1989). Daily ET rates on rainless days have been reported to be independent of elevation (Körner *et al.,* 1989; Körner 2003; Wieser *et al.,* 2008). Three reasons have been put forward to explain this: (1) steeper water vapour pressure gradients because of relatively higher surface temperatures,(2) enhanced contributions of evaporation from the soil surface at high elevation because of larger fractions of open ground (Kelliher *et al.,* 1995), and (3) stomatal downregulation of transpiration during periods of reduced moisture availability related to overall lower precipitation to ET ratios at low elevation, have been considered (Körner and Mayr, 1981; Körner, 2003).

Climatic effects on elevational changes in ET are well represented in models (*e.g.* McVicar *et al.,* 2007). However, the influence of elevational changes in plant canopy characteristics on ET has not received the same attention. Here, we aim at quantifying the separate influences of atmospheric conditions and vegetation on ET rates along an elevational gradient. For this purpose, we employed atmometers (often referred to as evaporimeters), a physics based probe (FAO Penman-Monteith model) and two types of grassland lysimeters (defined containers with vegetated soil monoliths) positioned along a 1 km elevational gradient. We present ET rates for rainless days from weighable lysimeters (WL) and for longer time periods (identical periods at all sites) from deep

seepage collectors (DSC). At both daily time scales and across longer time spans (close to 3 months during the growing season), we expect atmospheric evaporative demand to decrease with elevation as air temperature and VPD decline. However, for the reasons discussed above, we expect grassland evapotranspiration rates to be unaffected by elevation when equal sampling periods are compared (days or months). To test these hypotheses, we selected grassland types that are typically found along elevational gradients (from the montane to the alpine belt) in the Swiss Alps.

Material and methods

In order to determine the relative influences of vegetation structure and atmospheric conditions to evapotranspiration rates in different grassland types along an elevational gradient, we set up an experiment at three sites, all approximately 500 meters of elevation apart. The three sites are all located in the Ursern valley in the Swiss central Alps on more or less level terrain. The low site (L) at 1490 m a.s.l. (46°36'N, 8°32'E) had a loamy sand soil and a mean plant canopy height between 15 and 20 cm (always disregarding the height of inflorescences). The mid elevation site (M) at 1960 m a.s.l. (46°35'N, 8°29'E), had a partly podsolized brown earth soil and a mean canopy height of approximately 15 to 20 cm as well. The high elevation site (H) at 2440 m a.s.l. (46°34'N, 8°25'E), had a shallower, partly podsolized alpine brown earth soil and mean vegetation height varied between 5 and 10 cm. Currently, the potential climatic treeline in the Ursern valley lies between 2000 to 2100 m of elevation.

Each site was equipped with a weather station (Vantage Pro 2, Davis Instruments Corporation, Hayward, CA, USA) including a tipping bucket rain gauge, a cup anemometer, shielded air temperature and humidity sensors and a solar radiation sensor. Sensors were mounted at 1.5-1.8 m above the ground and data were recorded at 10-minute intervals. For all water balance calculations (DSCs), we used data from an additional rain gauge (RAINEW, Rainwise Inc., Barharbor, ME, USA) installed at 0.4 m above ground in the vicinity of DSCs, because rainfall measurements at greater height might underestimate true precipitation, especially under windy conditions (Duchon and Essenberg, 2001). We calculated Penman-Monteith evapotranspiration (PMET) assuming a similar short stature 'crop' for all sites. The PMET calculations were parameterized with daily mean climatic values for the comparison with long-term DSC readings, and with hourly means for daytime-only, when we compare PMET with ET rates of weighable lysimeters. Air pressure was calculated from elevation using equation 1 (Allen *et al.,* 1998). Daytime-only and daily (24h) PMET rates were calculated following Allen *et al.,* (1998):

$$P = 101.3 \left(\frac{293 - 0.0065\, z}{293} \right)^{5.26}$$ Equation 1

$$PMET = \frac{0.408\, \Delta\, (R_n - G)}{\Delta + \gamma(1 + C_d\, u_{1.8})} + \frac{\gamma \left(\frac{C_n}{T+273} \right) u_{1.8}\, (e_s - e_a)}{\Delta + \gamma(1 + C_d\, u_{1.8})}$$ Equation 2

where P is the atmospheric pressure in kPa, z is the elevation above mean sea level in m; Δ is the slope of the saturation vapour pressure ~ temperature curve in kPa °C^{-1}; R_n is the net radiation in MJ m^{-2} d^{-1} (calculated following FAO Irrigation and drainage paper 56 guidelines); G is the soil heat flux in MJ m^{-2} d^{-1} (calculated following FAO56 guidelines); γ is the psychrometric constant in kPa °C^{-1}; $u_{1.8}$ is the weather station wind speed in m s^{-1} (not corrected for measuring height); T is the mean daily air temperature in °C (true mean, not calculated from minimum and maximum air temperature); e_s is the saturation vapour pressure in kPa; e_a is the actual vapour pressure in kPa; C_n and C_d are the numerator and the denominator constants. For daily PMET rates, C_n and C_d were assumed to be 900 and 0.34, respectively. Daytime-only PMET was calculated by summing hourly PMET rates and using C_n=37 and C_d=0.24, respectively (Allen *et al.,* 2006; Walter *et al.,* 2000).

We used atmometers (type A, ETgage company, Loveland, CO, USA) to directly measure atmospheric evaporative demand at all three sites. An atmometer is a canvas covered Bellani plate (style #54, green canvas cover) that draws distilled water from a reservoir. The amount of water lost from the ceramic plate gives an integrated measure of the climatic influences on evaporation (Livingston, 1935). Evaporation pans are usually employed for this purpose, but these suffer from a number of drawbacks, such as stored heat or shelter effects by the pan's rim (Thom *et al.,* 1981). Atmometers do not store heat and are fully exposed to atmospheric circulation, but the ceramic and glass parts break when freezing, and rain causes a film of water on the canvas cover that suppresses atmometer evaporation (Chen and Robinson, 2009; Irmak *et al.,* 2005). For these reasons, atmometer measurements were only compared to daytime ET rates from WLs. Each site was equipped with one atmometer positioned 50 cm above the ground.

Weighable, monolithic lysimeters were set up at all sites (autumn 2008 at H, spring 2009 at L and M). Each lysimeter consisted of an inner bucket (diameter 28 cm, depth 22 cm) with a perforated bottom and an outer bucket (diameter 29 cm, depth 32 cm). The outer bucket keeps the inner bucket clean and allows easy lysimeter handling during weighing. It has been shown previously that lysimeters of such dimensions produce reliable data for high elevation terrain in a humid climate (Körner *et al.,* 1989). Monoliths were collected from representative patches of vegetation from each site and trimmed to tightly fit into the inner buckets. The soil surface of the monoliths reached up to 1.5 to 2.0 cm below the bucket's rim, thus preventing lateral water flow. Monoliths were selected from three typical, but different vegetation types for each elevation. 'Grass' lysimeters at L and M were dominated by an array of Poaceae (*e.g.* species of *Poa, Deschampsia* and *Festuca*) and by Cyperaceae at H (*Carex curvula* [ALL.]). Since the perennial bunch grass *Nardus stricta* (L.) occured at all three elevations, this offered the possibility to establish '*Nardus*' lysimeters at all three sites. In addition, we used 'herb' lysimeters, dominated by a suite of herbaceous species, mainly species of *Asteraceae, Rosaceae* and *Fabaceae* at all three sites. In the following, these three vegetation types will be referred to as grass, *Nardus* and herb. We installed 4 weighable lysimeters (WL) of each vegetation type at L and M, and 8 WLs per type at H, 48 WLs in total. In order to not disturb the natural canopy aerodynamics, WLs were positioned in the field such that the vegetation of each lysimeter matched the vegetation of its surroundings. WLs were watered on three occasions (16 mm of water per event) at L and M as a precautionary measure during longer rainless periods (no risk at H), since we were not interested in plant canopy responses to the weather peculiarities of a given season but rather the relative contribution of evaporative forcing and vegetation structure.

Atmometer evaporation (AE) and weighable lysimeter evapotranspiration (WLET) were measured during 12 clear days with no rain during the summer of 2010. WLET and AE were measured by weighing atmometers and weighable lysimeters in the field on an electrical balance placed in a wind free shelter (BBK422-35LA, precision ± 0.1 g,

Mettler-Toledo Inc., Greifensee, Switzerland at L and M; Precisa IBK 2400D, precision ± 0.1 g, Precisa Gravimetrics AG, Dietikon, Switzerland at H). Weighing was performed twice daily, once in the early morning before local sun rise and once in the evening shortly after local sun set. From the weight differences between morning and evening, we calculated daytime ET and atmometer evaporation. At the end of the experiment, all atmometers were weighed jointly at H during 7 days in order to assess potential differences in AE among individual atmometers, but there were none. We use the word clear here to describe weather conditions during WLET measuring days, although, the sky was not always perfectly clear. Clear-sky days occur only rarely in the test region.

For measuring ET rates across longer time spans, DSCs were constructed and installed at H in summer 2006, and at L and M in spring 2009. A deep seepage collector is a stainless steel bucket (diameter 25 cm, depth 40 cm) with a perforated steel plate 10 cm above the bucket's bottom. A monolith rests on top of a piece of filter cloth on the perforated steel plate. The bucket's rim reached 1.5 to 2 cm above the monolith and the surrounding soil, again in order to prevent lateral runoff and inflowing water from the surrounding area. Seepage water was collected through a PVC pipe that provided access to the volume below the monolith using a mobile pump. DSCs were filled with the same vegetation types as the weighable lysimeters (similar plant species composition). At each site, 4 DSCs (6 for herb at H) were built of each vegetation type, 38 DSCs in total. DSCs were placed in similar vegetation in order not to disturb the natural canopy aerodynamics. Similar to the weighable lysimeters, deep seepage collectors at L and M received precautionary watering (21 mm of water per event, L 2010: 3x, L 2011: 4x; M 2010: 3x, M 2011: 2x). ET from DSCs (DSCET) was calculated for long time spans using the water balance equation:

$$P = R + ET + \Delta S \qquad \text{Equation 3}$$

where P stands for the amount of precipitation (including added water), R for total runoff, ET for evapotranspiration and ΔS for the difference in soil moisture content (all in mm). Differences in soil moisture content were assumed to be negligible for longer

time periods between two dates on which rainfall exceeded the water storage capacity of the soil. DSCET was thus calculated for a time period of 86 and 79 days during the growing seasons of 2010 and 2011, respectively. DSCET was compared with PMET only (given the problems with atmometer wetting after rain events as discussed above).

At the end of the experiment, above-ground phytomass was harvested from all WLs and DSCs and sorted into live and dead parts, and phanerogams *versus* cryptogams (mosses and lichens). LAI was calculated from biomass and specific leaf area of sub-samples (leaf area per g dry matter, SLA) determined with a leaf area meter (LI 3100, LI-COR, Lincoln, NE, USA). Afterwards, plant samples were oven dried for 48 hours at 80 °C and weighed. Monoliths of all weighable lysimeters were oven dried at 100 °C for 14 days in order to reconstruct soil water content for every weighing event (percentage of volumetric water content at saturation, which was assumed to be the water content at the highest recorded lysimeter weight).

Statistics

Statistical analyses and calculations were performed using the open-source software R, version 2.15.0 (R Development Core Team, 2010). For weighable lysimeters and deep seepage collectors, mean evapotranspiration rates were calculated across all days. Mean atmometer evaporation (AE) and PMET rates were calculated for each site across all days. The influence of elevation on ET rates was analysed using the "car" package (Fox and Weisberg, 2011). Non-parametric tests were used in case data were not normally distributed after data transformations (Kruskal-Wallis test). Post hoc multiple comparisons were performed using the "multcomp" (Hothorn *et al.,* 2008) and the "sandwich" (Zeileis, 2004; Zeileis, 2006) libraries following procedures as outlined in Herbrich and co-authors (2010). Differences between means were considered statistically significant at $p<0.05$. Regression calculation was applied to WLET/AE ratios in order to test the influence of soil moisture contents on WLET.

Results

During 12 clear days all 48 WLs were weighed at all sites. During these days, daytime air temperature decreased by -4.8 K km^{-1} between L and M and by -7.6 K km^{-1} between M and H. Across the entire elevational gradient, daytime air temperature decreased by -6.2 K km^{-1} (Table 1). Decreases in daytime air temperature thus match air temperature trends that are generally observed along such elevational gradients in summer (-6.0 K km^{-1}; Dodson and Marks, 1997; Rolland, 2003). Differences in mean daytime vapour pressure deficit between L and M were approximately as large as between M and H (L: 0.67 ± 0.25 kPa; M: 0.57 ± 0.21 kPa; H: 0.50 ± 0.11 kPa). Daytime wind speeds were slightly higher at H than at L and M (L: 2.1 ± 0.5 m s^{-1}; M: 2.2 ± 0.9 m s^{-1}; H: 3.0 ± 1.0 m s^{-1}), likely, as a result of more sheltered conditions at the two lower sites. Daytime sums of incoming solar radiation varied strongly between days, but means across all days were very similar at the three sites (L: 24.4 ± 3.7 MJ d^{-1}; M: 24.4 ± 4.5 MJ d^{-1}; H: 25.5 ± 3.1 MJ d^{-1}).

Table 1. Minimum, mean (± sd) and maximum of daytime weather conditions at L, M and H over the 12 bright days of WLET measurements.

Site	Air temperature			Wind speed			Solar radiation			VPD		
elevation (m a.s.l.)	min	mean (°C)	max	min	mean ($m\ s^{-1}$)	max	min	mean ($MJ\ d^{-1}$)	max	min	mean (kPa)	max
H (2440)	8.0	12.1±2.2	14.6	1.7	3.0±1.0	4.7	20.2	25.5±3.1	29.8	0.34	0.50±0.11	0.67
M (1960)	11.3	15.8±2.9	19.4	1.1	2.2±0.9	4.7	15.5	24.4±4.5	30.3	0.29	0.57±0.21	0.96
L (1490)	12.4	18.0±3.2	22.1	1.6	2.1±0.5	3.1	18.7	24.4±3.7	29.5	0.23	0.67±0.25	0.98

Across all 12 days, atmometer evaporation (AE) decreased significantly with elevation (Table 2; $F_{2,33}$=5.06; p=0.012). Between L and M, AE decreased by 1.0 mm km^{-1} (-20% km^{-1}; low site ratios for AE), between M and H, AE declined by 1.3 mm km^{-1} (-30% km^{-1}). Across the entire elevational gradient, AE decreased by 1.1 mm km^{-1} (-24% km^{-1}).

Table 2. Mean daytime AE and PMET (± sd), mean AE/PMET (± sd) on the 12 bright days of WLET measurements at L, M and H. Low site ratios for AE (AE at a site divided by AE at L; AE_{site}/AE_{low}) and PMET (PMET at a site divided by PMET at L; $PMET_{site}/PMET_{low}$).

	AE mm d^{-1}	PMET mm d^{-1}	AE/PMET	AE_{site}/AE_{low}	$PMET_{site}/PMET_{low}$
H	3.7±0.6#^{b}	3.9±0.5^{a}	0.94±0.03^{b}	0.77	0.89
M	4.3±0.8^{ab}	4.0±0.9^{a}	1.07±0.09^{a}	0.91	0.92
L	4.7±1.0^{a}	4.4±0.8^{a}	1.08±0.07^{a}	1.00	1.00

sd values in AE do not reflect error, but variability across days.

Note: values with different letters indicate significant differences between sites at p<0.05

Besides absolute AE rates, variability in AE diminished with elevation. Solar radiation and mean daytime air temperature (and related VPD) explained most of the variability in daytime AE (multivariate R^2 adj.=0.91, F(3, 66)=227.40, p<0.001; the model includes AE rates from additional days, 69 atmometer measurements in total). Daytime AE for rainless days was best predicted by using the following simple regression:

$$AE = -1.51 + 0.19 \times T_{mean} - 0.05 \times T_{min} + 0.14 \times S_{rad} \qquad \text{Equation 4}$$

Here, AE is expressed in mm d^{-1}, T_{mean} and T_{min} are the mean and minimum daytime air temperature in °C and S_{rad} is incoming solar radiation in MJ d^{-1}.

The reduction in PMET (-11% km^{-1}) was less pronounced than the decrease in AE and was not significant across all sites for those 12 clear days (Table 2; $F_{2,33}$=1.19; p=0.319).

The decline was not consistent across the transect with a larger change between L and M (-16% km^{-1}) and a less pronounced change between M and H (-7% km^{-1}). Thus, PMET results contrast AE signals, which changed relatively less between L and M (-20% km^{-1}), but were more pronounced between M and H (-30% km^{-1}). Consequently, AE to PMET ratios (AE/PMET) were significantly different at H compared to L and M ($F_{2,33}$=14.97; p<0.001). AE was higher than PMET at L and M, but lower than PMET at H. In other words, AE and PMET, both reflecting atmospheric evaporative demand only (though slightly different) decreased with elevation, but the actual reduction in ET was more pronounced indicating that physical factors and plant canopy characteristics add up and cause the elevational decline in ET to exceed predictions.

During the selected days, soil moisture content in weighable lysimeters was high (mean soil moisture as a percentage of saturated soil moisture content: L: 66 ± 18%; M 67 ± 19%; H: 79 ± 12%), and WLET to AE ratios were generally unrelated to soil moisture content (regressions not shown). We therefore assume that soil moisture content did not limit WLET at any of the three sites. WLET rates, averaged across all 12 days, declined with elevation (Fig. 1; Table 3). When lysimeters of all plant cover types were taken together (Overall), WLET was significantly affected by site ($F_{2,45}$=105.76; p<0.001). The elevational decline in WLET was similar in magnitude for herb and grass dominated WLs along the entire elevational gradient (-37% and -41% in grass and herb dominated WLs; low site ratios for WLET), but it was slightly less pronounced for *Nardus* dominated lysimeters (-31%). WLET rates across all three vegetation types decreased by 14% between L and M (grass: -17%; herb: -11% and *Nardus*: -14%) and by 23% between the M and H (grass: -30%; herb: -30% and *Nardus*: -17%; Table 3, Fig. 1).

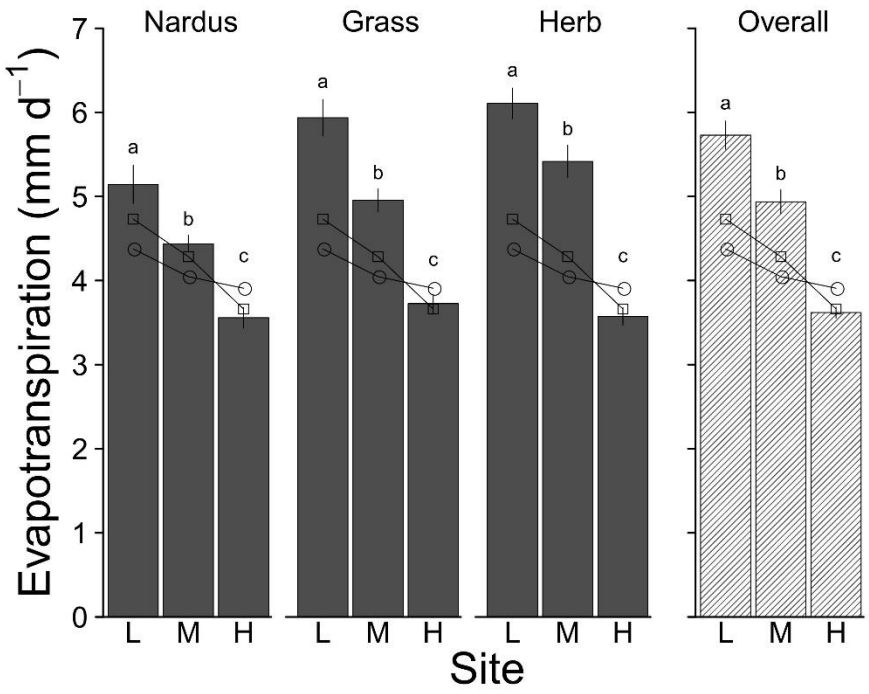

Figure 1. Mean daily WLET at the L, M and H for vegetation types separately and for all vegetation types combined. Squares indicate mean AE and circles mean PMET. Different letters indicate significant differences (at $p<0.05$). Note that within a site all vegetation types experience the same AE and PMET.

Table 3. Mean WLET rates (± sd) and low site ratios for WLET (WLET at a site divided by WLET at L: $WLET_{site}/WLET_{low}$; ± sd) for single vegetation types and for all vegetation types combined (number of replicates in brackets) on the 12 selected days. Also we present WLET divided by AE (WLET/AE; ± sd) and WLET divided by PMET (WLET/PMET; ± sd). Different letters indicate significant differences (at $p<0.05$) between sites (within site differences among vegetation types are not considered).

Site	Vegetation	WLET (mm d^{-1})	$WLET_{site}/WLET_{low}$	WLET/AE	WLET/PMET
H	*Nardus* (8)	3.6±0.3^{c}	0.69±0.07	0.97±0.09^{a}	0.91±0.09^{b}
	Grass (8)	3.7±0.3^{c}	0.63±0.05	1.01±0.09^{b}	0.95±0.08^{b}
	Herb (8)	3.6±0.3^{c}	0.59±0.05	0.98±0.08^{b}	0.91±0.08^{b}
	Overall (24)	3.6±0.3^{c}	0.63±0.06	0.99±0.09^{b}	0.92±0.08^{b}
M	*Nardus* (4)	4.4±0.2^{b}	0.86±0.04	1.02±0.05^{a}	1.09±0.05^{a}
	Grass (4)	5.0±0.3^{b}	0.83±0.05	1.15±0.07^{ab}	1.22±0.08^{a}
	Herb (4)	5.4±0.4^{b}	0.89±0.06	1.26±0.09^{a}	1.34±0.10^{a}
	Overall (12)	4.9±0.5^{b}	0.86±0.09	1.14±0.12^{a}	1.21±0.13^{a}
L	*Nardus* (4)	5.1±0.5^{a}	1.00±0.09	1.09±0.10^{a}	1.17±0.11^{a}
	Grass (4)	5.9±0.4^{a}	1.00±0.07	1.26±0.10^{a}	1.35±0.10^{a}
	Herb (4)	6.1±0.4^{a}	1.00±0.06	1.30±0.08^{a}	1.39±0.08^{a}
	Overall (12)	5.7±0.6^{a}	1.00±0.10	1.22±0.13^{a}	1.30±0.13^{a}

WLET rates were 22% and 14% larger than AE at L and M, but at H, WLET was similar to AE (1% smaller). For all vegetation types together, WLET/AE ratios, were significantly lower at H compared to L and M ($F_{2,45}=21.47$; $p<0.001$; Fig. 2). Only for *Nardus* lysimeters, WLET/AE ratios did not vary significantly among sites, underlining that the type of plant cover was the main driver of these differences. WLET to PMET ratios (WLET/PMET) were above unity at L and M (L: 1.30 ± 0.13; M: 1.21 ± 0.13), while at H, these values were below unity (0.92 ± 0.08; Fig. 2). Overall, WLET/PMET ratios were significantly influenced by elevation ($F_{2,45}=59.70$; $p<0.001$), and significantly reduced at H in comparison to M and L, both, within each vegetation type and for all vegetation types combined (Table 3). So, PMET greatly underestimated actual ET at L and M, and overestimated it at H.

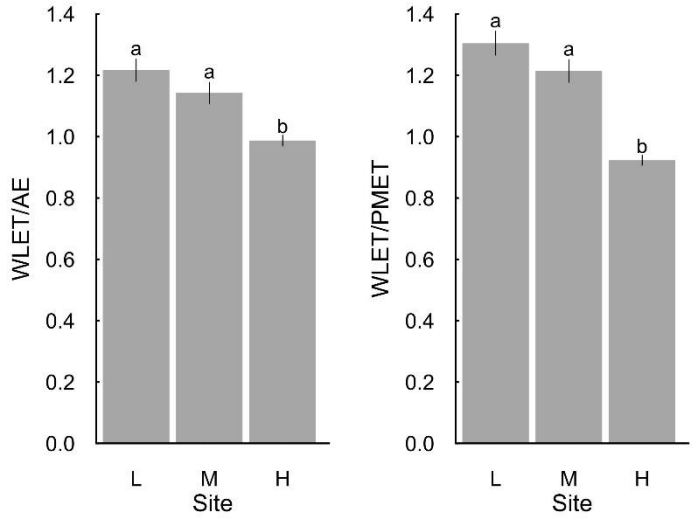

Figure 2. WLET to AE (WLET/AE) and WLET to PMET (WLET/PMET) at L, M and H for vegetation types combined. Different letters indicate significant differences (at $p<0.05$).

Mean vascular plant biomass in weighable lysimeters differed significantly between sites ($F_{2,44}=30.40$; $p<0.001$) and was significantly lower at H in comparison to L and M across all vegetation types (Table 4). LAI was strongly reduced at H (rough LAI estimates: L: 5.1; M: 5.4; H: 2.1, data not shown). Dead plant material (necromass and litter) did not differ significantly among sites ($F_{2,44}=0.97$; $p=0.386$). WLET/AE ratios were positively related to vascular plant biomass (Fig. 3). All vegetation types showed a positive, linear relationships between vascular plant biomass and WLET/AE, and the slope of the regression was steepest in grass and herb and slightly less steep in *Nardus* WL (grass: R^2 adj.=0.76, $F(1, 14)=44.1$, $p<0.001$; herb: R^2 adj.=0.73, $F(1, 14)=37.9$, $p<0.001$; *Nardus*: R^2 adj.=0.19, $F(1, 13)=4.3$, $p<0.05$; overall: R^2 adj.=0.45, $F(1, 45)=38.6$, $p<0.001$). In addition, vascular plant biomass was positively related to WLET/PMET ratios (overall: R^2 adj.=0.55, $F(1, 45)=57.5$, $p<0.001$; data not shown). Cryptogam mass differed significantly among sites ($F_{2,44}=13.76$, $p<0.001$) and was significantly higher at H (due to higher abundance of lichens) in comparison to the other two sites (Table 4), but showed no correlation with any of the ET measures.

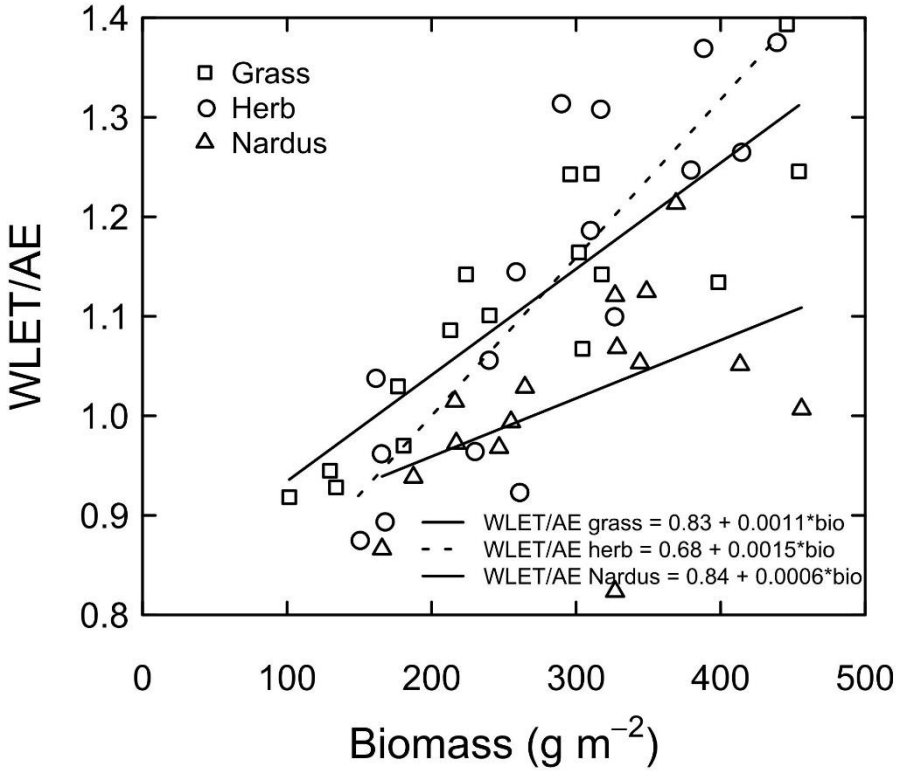

Figure 3. WLET to AE ratios (WLET/AE) for each lysimeter as depending on vascular plant biomass.

Table 4. Characterisation of vegetation structure in WLs and DSCs: vascular plant biomass, necromass (standing dead plant material and litter) and cryptogam mass (g m^{-2}; mean ± sd) at L, M and H. Different letters indicate significant differences between sites (within vegetation types).

Site	Vegetation type	WL			DSC		
		Biomass (g m^{-2})	Necromass (g m^{-2})	Cryptogams (g m^{-2})	Biomass (g m^{-2})	Necromass (g m^{-2})	Cryptogams (g m^{-2})
H	*Nardus*	245±60^{b}	263±118^{a}	49±84^{a}	273±60^{a}	393±75^{a}	22±9^{a}
	Grass	175±50^{b}	143±55^{a}	116±97^{b}	182±55^{b}	204±91^{b}	243±230^{a}
	Herb	212±62^{b}	149±43^{a}	129±64^{b}	226±74^{b}	268±56^{ab}	59±63^{a}
	Overall	210±62^{b}	185±94^{a}	98±87^{b}	227±69^{b}	289±107^{b}	108±160^{a}
M	*Nardus*	361±93^{a}	130±186^{a}	7±13^{a}	361±49^{a}	375±98^{a}	31±27^{a}
	Grass	369±71^{a}	85±80^{a}	2±2^{a}	442±49^{a}	295±46^{b}	17±19^{a}
	Herb	359±69^{a}	274±60^{a}	0±0^{a}	368±36^{a}	226±59^{b}	1±1^{a}
	Overall	363±71^{a}	163±139^{a}	3±8^{a}	390±63^{a}	299±90^{b}	16±22^{a}
L	*Nardus*	354±13^{ab}	72±2^{a}	0±0^{a}	423±132^{a}	572±149^{a}	7±7^{a}
	Grass	339±72^{a}	95±67^{a}	0±0^{a}	363±70^{a}	452±92^{a}	3±1^{a}
	Herb	338±68^{a}	215±43^{ab}	0±0^{a}	433±25^{a}	348±16^{a}	13±17^{a}
	Overall	342±55^{a}	132±80^{a}	0±0^{a}	406±85^{a}	457±133^{a}	8±10^{a}

For the whole period during which DSCs were operational at all elevations (approximately 3 months), mean daily air temperatures (24 h) decreased with elevation by -5.4 K km^{-1} (2010 and 2011) between L and M. Between M and H, air temperature lapse rates were 7.0 K km^{-1} and 6.0 K km^{-1} for 2010 and 2011, respectively (Table 5). The highest amounts of rainfall were recorded at H during the 2010 season (497 mm) and lower amounts at L (360 mm) and M (371 mm). In 2011, rainfall was highest at M (418

mm) and only slightly lower at H (397 mm) and L (311 mm). The number of days with rainfall (51 d in both years) did not increase with elevation and was similar at all sites (Table 5). Precipitation, including amounts watered, was clearly in excess of ET at all locations.

Table 5. Mean daily weather conditions (mean ± sd) at L, M and H during the DSC sampling periods of 2010 and 2011 (operational from - until). Minimum, mean (± sd) and maximum air temperature and mean daily values for wind speed, solar radiation and VPD (± sd). Precipitation column presents rainfall (r), rainfall and added water (r+w) and the number of rainy days (days with >0.2 mm precipitation) during the sampling period (rd).

Site	Year	operational from	operational until	Air temperature min	Air temperature mean (°C)	Air temperature max	Wind speed ($m\ s^{-1}$)	Solar radiation ($MJ\ d^{-1}$)	VPD (kPa)	Precipitation r (mm)	Precipitation r+w (mm)	Precipitation rd (d)
H	2010	16/06/2010	10/09/2010	-4.7	6.8±4.3	19.9	2.4±1.0	18.4±7.9	0.30±0.19	497	497	52
	2011	20/06/2011	07/09/2011	-2.6	7.3±3.9	19.6	2.3±0.9	19.2±7.2	0.33±0.21	397	397	49
M	2010	15/06/2010	09/09/2010	-1.2	10.2±4.2	24.1	2.1±0.9	18.9±7.9	0.35±0.24	371	432	50
	2011	20/06/2011	07/09/2011	-0.9	10.2±3.9	23.2	1.9±0.9	19.5±7.3	0.37±0.24	418	459	53
L	2010	15/06/2010	09/09/2010	-1.4	11.9±3.7	28.3	1.9±1.0	19.0±7.4	0.47±0.28	360	421	52
	2011	20/06/2011	07/09/2011	0.3	12.4±3.3	27.5	1.5±0.7	18.4±7.1	0.47±0.27	311	393	51

During both DSCET measuring periods, mean daily PMET decreased with elevation (Table 6), however, differences among sites were again weak and not statistically significant (Kruskal Wallis test, $X^2(2)=4.56$; $p=0.103$). Mean daily PMET decreased by 5% between L and M and by 9% between M and H during 2010. For 2011, a year with a smaller air temperature lapse rate, elevational reductions in PMET were also smaller from L to M (-2%) and from M to H (-4%). Averaged across both seasons, the reduction in PMET was 10% along the entire elevational gradient.

Mean daily DSCET for the 86 d sampling period of 2010, averaged for all vegetation types, was significantly influenced by elevation (Kruskal Wallis test, $X^2(2)=23.52$; $p<0.001$; Table 6). For that season, DSCET at L (3.7 mm d^{-1}) was significantly higher than DSCET at M (2.1 mm d^{-1}) and H (2.0 mm d^{-1}), despite the fact that all sites received very similar amounts of solar radiation. DSCET rates thus decreased by 43% between L and M and by only 2% between M and H. For the 79 d sampling period of 2011, mean daily DSCET also varied significantly with elevation ($F_{2,34}=37.4$; $p<0.001$). Again, DSCET rates were significantly higher at L (3.3 mm d^{-1}) compared to M (2.7 mm d^{-1}) and H (2.5 mm d^{-1}). Overall DSCET rates dropped by 19% between L and M and by 6% between M and H. Taking both seasons together, DSCET rates decreased by 35% from L to H.

Table 6. Mean daily DSCET rates (± sd; number of replicates in brackets) for all three vegetation types at L, M and H for 2010 and 2011. Mean PMET (± sd across days) at each site during the sampling period. Low site ratios for PMET ($PMET_{site}/PMET_{low}$) and DSCET (mean DSCET of a vegetation type divided by mean DSCET of the same vegetation type at the low site; $DSCET_{site}/DSCET_{low}$) and DSCET to PMET ratios (DSCET/PMET; mean ± sd). Different letters indicate significant differences.

Site	Year	DSCET (mm d $^{-1}$)				PMET (mm d^{-1})	$PMET_{site}/PMET_{low}$	$DSCET_{site}/DSCET_{low}$				DSCET/PMET			
		Nardus	Grass	Herb	Overall			*Nardus*	Grass	Herb	Overall	*Nardus*	Grass	Herb	Overall
H	2010	2.01±0.14^{b}(4)	2.04±0.18^{b}(3)	2.04±0.07^{b}(6)	2.03±0.11^{b}	2.6±1.2#^{a}	0.86	0.56	0.51	0.61	0.55	0.76±0.06^{b}	0.77±0.07^{b}	0.77±0.03^{b}	0.76±0.04^{b}
	2011	2.49±0.34^{b}(4)	2.43±0.08^{b}(3)	2.44±0.14^{b}(6)	2.45±0.20^{b}	2.8±1.0^{a}	0.94	0.78	0.74	0.73	0.75	0.89±0.12^{a}	0.87±0.03^{b}	0.87±0.05^{b}	0.87±0.07^{b}
M	2010	2.00±0.32^{b}(4)	2.44±0.13^{b}(4)	1.73±0.24^{b}(3)	2.09±0.37^{b}	2.9±1.3^{a}	0.95	0.55	0.61	0.52	0.57	0.69±0.11^{b}	0.84±0.05^{b}	0.60±0.09^{b}	0.72±0.13^{b}
	2011	2.77±0.24^{b}(4)	2.70±0.25^{b}(4)	2.48±0.42^{ab}(4)	2.65±0.31^{b}	2.9±1.1^{a}	0.98	0.87	0.82	0.75	0.81	0.94±0.08^{a}	0.92±0.08^{ab}	0.85±0.15^{a}	0.90±0.11^{b}
L	2010	3.62±0.33^{a}(4)	4.02±0.32^{a}(4)	3.33±0.32^{a}(4)	3.66±0.41^{a}	3.1±1.2^{a}	1.00	1.00	1.00	1.00	1.00	1.18±0.11^{a}	1.31±0.11^{a}	1.08±0.11^{a}	1.19±0.14^{a}
	2011	3.19±0.21^{a}(4)	3.28±0.23^{a}(4)	3.32±0.22^{a}(4)	3.26±0.21^{a}	3.0±1.0^{a}	1.00	1.00	1.00	1.00	1.00	1.07±0.07^{a}	1.10±0.08^{a}	1.12±0.07^{a}	1.10±0.07^{a}

#Note: sd of PMET reflects variability through time rather than error.

At L, DSCET rates surpassed mean PMET, while at both M and H, DSCET rates were lower than PMET (Fig. 4). Across all vegetation types, elevation significantly affected DSCET/PMET ratios in both seasons (2010: Kruskal Wallis test, $X^2(2)=23.57$; $p<0.001$; 2011: $F_{2,34}=25.58$; $p<0.001$). For both seasons, DSCET/PMET ratios were significantly lower at M and H compared to L. DSCET/PMET ratios for both seasons (2010/2011) were 1.19/1.10 at L, 0.72/0.90 at M, and 0.76/0.87 at H. Thus, also for longer time spans, elevational reductions in DSCET were always larger than reductions predicted by the Penman-Monteith model.

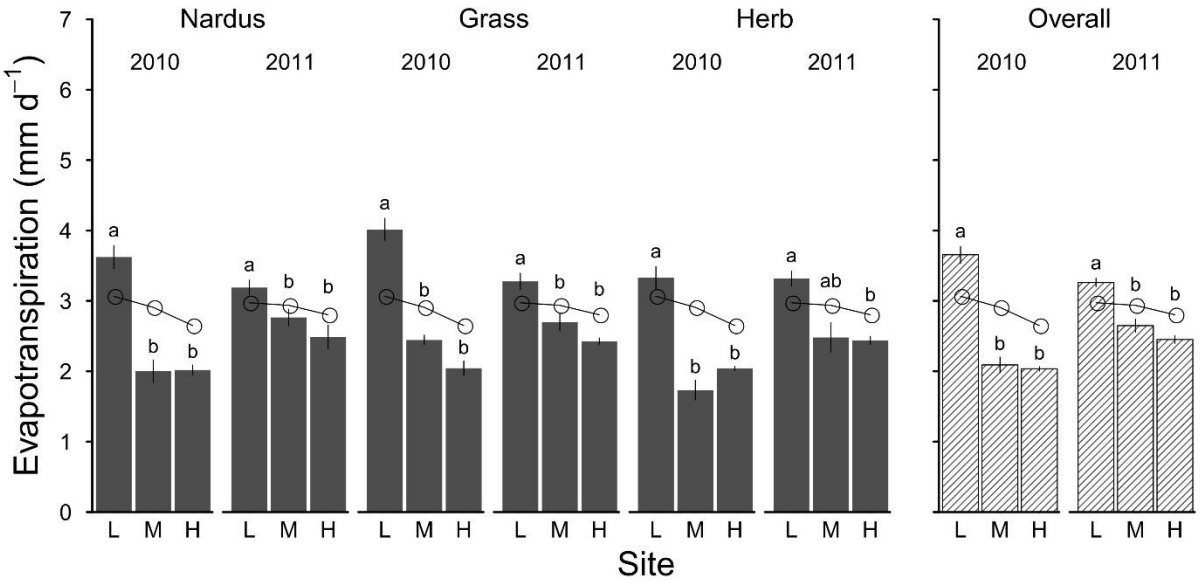

Figure 4. Mean daily DSCET at the L, M and H for the growing seasons of 2010 and 2011 for vegetation types separately and for all vegetation types combined (Overall). In circles, mean PMET as calculated for the sampling period for each site. Different letters indicate significant differences (at $p<0.05$).

Similar to weighable lysimeters, vascular plant biomass in DSCs decreased significantly with elevation (Table 4; ($F_{2,33}=22.06$; $p<0.001$). Vascular plant biomass was significantly higher at L and M compared to H. Unlike in WLs, dead plant material (necromass and litter) in DSCs was higher at L and significantly reduced at both M and H ($F_{2,33}=8.68$; $p<0.001$). Cryptogam mass in DSCs did not reveal a consistent trend with elevation.

Discussion and conclusions

By combining results obtained with a meteorological model (PMET), atmometers (AE), weighable lysimeters (WLET) and deep seepage collectors (DSCET), we have demonstrated that evapotranspiration decreases with elevation. Trends in ET were essentially the same for clear days (WLET: -37% from L to H) as for a *c.* three-month period including all weather conditions (overall DSCET: -35% from L to H). Consistently, elevational decreases in AE and PMET were smaller than elevational declines in WLET and DSCET. Thus, the results counter earlier suppositions that annual ET decreases with elevation due to reduced season length only, with no significant difference in daily mean ET (*e.g.* Körner *et al.,* 1989; Wieser *et al.,* 2008). Clearly, reductions in the density and height in plant cover with elevation are a major driver of the observed elevational reductions in ET. Apparently, effects of enhanced soil evaporation due to lower LAI and steeper canopy to free air temperature gradients do not fully compensate the effect of reduced plant biomass and reduced atmospheric evaporative demand at high elevation. Presumably, the earlier transect studies reporting ET not to be affected by elevation at daily time scales, have included lowland locations where limited soil moisture (due to lower precipitation to evapotranspiration ratios) and high VPD have reduced ET through stomatal regulation.

The WL and DSC experiments were performed under conditions where soil moisture did not limit ET rates. With precipitation ranging from 1500 mm at L to 1900 mm a^{-1} at H, water availability generally does not limit ET in the study area (cf.Calanca, 2004). Physiological restrictions to ET from limited soil moisture during the experiment would thus have constituted a momentary peculiarity. WLET and DSCET rates reported here can therefore be considered potential ET rates. Exclusion of the influence of physiological restrictions to ET makes that the reported trends mirror elevational changes in atmospheric forcing and canopy characteristics only.

Altitudinal trends in climatic parameters during WLET and DSCET measurements largely matched general altitudinal patterns (McVicar *et al.,* 2007; Marty *et al.,* 2002).

Therefore, for mountain regions in general, trends in atmospheric evaporative demand similar to those reported here, may be expected. Although estimates from the Penman Monteith approach and atmometers differed slightly, atmospheric evaporative demand clearly decreased with elevation. Because trends in ET along the chosen transect strictly reflect changes in altitude-related atmospheric drivers and plant canopy characteristics (no gradient in effective plant available soil moisture), we can conclude that the altitudinal reduction in atmospheric evaporative demand, explains approximately half of the elevational decline in ET. The other half of the signal comes from elevational reductions in life plant biomass. While AE and PMET indicate that contributions to ET from climatic parameters steadily decrease with elevation, WLET/AE and WLET/PMET show that the decrease in ET due to reduced plant biomass mainly occurs between M and H (Fig. 2). For *Nardus* dominated lysimeters, ET rates declined less with elevation than in the other two vegetation types. This is probably the result of a less pronounced decline in plant biomass in *Nardus* dominated lysimeters as at L and M biomass was similar for herb, grass and *Nardus*, while at H, *Nardus* lysimeters had slightly higher biomass than herb and grass dominated lysimeters.

Since LAI at L and M was above 3 m^2 m^{-2}, and because canopy conductance has been suggested to saturate at LAI values above 3 (Schulze *et al.,* 1994; Hammerle *et al.,* 2008), we assume that WLET/AE and WLET/PMET ratios at L and M represent maximum values. Similar WLET/PMET ratios have been reported for winter wheat (Kjaersgaard *et al.,* 2008). Stable canopy conductance values at high LAI is confirmed by similar and high contributions to ET from the plant canopy at L and M and significantly lower canopy contributions at H.

DSCET is likely to be an underestimation of true ET, since tipping buckets may slightly underestimate rainfall (due to effects of wind and evaporation of rain from the tipping bucket). The DSCET rates presented here must therefore be considered conservative values. Errors in DSCET, caused by differences in soil water contents between the first and the last day on which DSCs were emptied, are likely to be small because of the

regular re-saturation of the soil and the relative length of the sampling period. Because DSCET was measured for the same calendar period (set by the snow free period at H) during both 2010 and 2011 at all sites, the elevational decline in DSCET cannot be explained by season length. Since the actual snow free period is longer at low elevation (in the central Alps, the length of the snow free period decreases by about 26 days km^{-1}; see Veit, 2002), season length effects will add to the elevational decline in annual ET (as for example compiled from several studies in Lang, 1981).

Along the elevational gradient, DSCET rates for 2010 dropped much more (-45%) than they did in 2011 (-25%). Climatic conditions before the sampling period may have contributed to this. The weather during the 2010 growing season was quite normal, but it started exceptionally early due to limited snowfall in the preceding winter. In contrast, the 2011 season started with a normal snowmelt date, but the summer was relatively wet. The 2011 sampling period had equal numbers of days with rain while the sampling period was one week shorter. The early onset of the season in 2010 may have enhanced DSCET more at L than at M and H (earlier peak biomass, longer day-length).

Our findings underline the importance of incorporating elevational changes in climate and plant cover data in hydrological models. ET models can be substantially improved by accounting for elevational changes in canopy characteristics within single land cover types especially in places where LAI values drop significantly below 3.0 (LAI at which canopy conductance has been shown to saturate, Schulze *et al.,* 1994). Such changes may be particularly important for land cover types occurring across vast elevational gradients as we have shown that, along such gradients the contribution of canopy characteristics to ET changes substantially. The Penman-Monteith approach and atmometers greatly underestimated ET at our montane, lower end of the transect, and overestimated ET in high alpine terrain. Therefore, ET estimates based solely on atmospheric forcing, are likely to overestimate ET and thus underestimate catchment runoff, for elevations above 2000 m a.s.l. while for elevations below 2000 m a.s.l., such models may underestimate ET. The simple model provided in equation 4 can be used for estimating AE from air temperature and solar radiation data. Realistic proxies that

capture the changing contribution of vegetation to ET with elevation have not been presented so far. Our data can be used to adjust AE or PMET to obtain realistic ET estimates for different grassland types in montane and alpine environments (WLET/AE L: 1.22 ± 0.13; M: 1.14 ± 0.12; H: 0.99 ± 0.09; WLET/PMET L: 1.30 ± 0.13; M: 1.21 ± 0.13; H: 0.92 ± 0.08). These WLET/AE and WLET/PMET ratios can be assumed to be representative for grassland at elevations similar to the elevations of our low, mid and high sites respectively.

Because the contribution of the canopy to ET positively depends on above-ground plant biomass, active management of the vegetation (*e.g.* through grazing or mowing), reduces ET and thus enhances catchment runoff. For H we previously found substantial reductions in ET due to simulated grazing (on average by -12% during clear days at H, Inauen *et al.,* 2013). The extent to which ET can be reduced through land use practices at lower elevations is likely to be more substantial because here, the contribution to ET from the plant canopy is larger. Finally, these data may serve as a benchmark for testing simulated ET rates for elevational gradients for environments where soil moisture does not affect ET rates (valid for many arctic and alpine settings).

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Chapter 3

Hydrological consequences of grassland abandonment along an elevational gradient in the Swiss Alps

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Abstract

Land use influences the ecosystem water balance. Abandonment of high elevation pastures and meadows leads to taller grass and/or dwarf shrub invasion. We investigated how this affects evapotranspiration (ET) and the catchment hydro-electric potential. In a high elevation catchment in the Swiss Alps, we employed a total of 139 weighable lysimeters (WL) to measure bright day ET (WLET), and 122 deep seepage collectors (DSC) to measure long-term ET (DSCET) at 1490 m (L-low), 1960 m (M-mid) and 2440 m a.s.l. (H-high) elevation. WLs and DSCs contained 20 L undisturbed monoliths, half of which were clipped to simulate grazing. Abandonment increased WLET by 15 to 37% at L and M, but only 3 to 6% at H. Larger abandonment effects at L and M resulted from higher biomass. At L, DSCET increased by 9 to 27% (18 to 54 mm) in 2010 and 2011. More humid conditions in combination with large biomass variation, prevented significant effects at M and H, that were however significant in a previous study. When results from this and previous studies were scaled to three elevational belts (L, M, H: 1400-1800, 1800-2200 and 2200-2600 m a.s.l.) of the upper Reuss catchment (Ursern valley, total surface area: 227 km²), we find that grazing cessation reduced runoff by 180 - 740 $m^3\ ha^{-1}\ a^{-1}$, a loss in hydro-electric potential of 30 to 135 CHF $ha^{-1}\ a^{-1}$ or 0.1 to 0.4 Mio CHF a^{-1} for the low belt (total grassland area: 1736 ha). For the middle belt (4965 ha of grassland), abandonment reduced runoff by 0 to 740 $m^3\ ha^{-1}\ a^{-1}$, 0 to 235 CHF ha^{-1} or 0 to 1.4 Mio CHF and for the high belt (6624 ha of grassland), effects ranged from 0 to 350 $m^3\ ha^{-1}\ a^{-1}$, 0 to 125 CHF ha^{-1} or 0 to 1.2 Mio CHF. We hence conclude that continued land use brings guaranteed but limited hydro-electric yields for low montane lands and that potentially, abandonment effects are much larger for high montane elevations due to greater falling height. Effects of falling height do not completely counter the smaller abandonment effects for alpine sites. For the valley as a whole, we find that land use adds between 0.1 to 2.9 Mio CHF (0.1 to 2.7 Mio EUR), depending on summer weather.

Keywords

Grazing, land use, evapotranspiration, catchment water yield, runoff, hydro-electric potential

Introduction

Transitions in vegetation as resulting from declining land use have been widely reported across the European Alps (Kräuchi *et al.*, 2000; Tappeiner *et al.*, 2008; Brändli, 2010; Körner, 2014). Between 1980 and 2000, 33% of all farms have been given up (Streifeneder *et al.*, 2007). Mainly high-elevation and steep grassland has been abandoned while at lower elevations land use has intensified (MacDonald *et al.*, 2000; Tasser *et al.*, 2005; Gellrich *et al.*, 2007; Monteiro *et al.*, 2011; Cocca *et al.*, 2012).

Land use practices play a crucial role in determining vegetation structure and composition (Niedrist *et al.*, 2009, Lueth *et al.*, 2011). Abandonment leads to the development of tall grass swards, the accumulation of dead plant material (Stöcklin and Gisi, 1989; Rosset *et al.*, 2001). After longer periods of neglect, dwarf shrubs invade abandoned pastures (Tappeiner and Cernusca, 1989; Wohlfahrt *et al.*, 2003; Gehring-Fasel *et al.*, 2009). These, in turn, are commonly followed by tall shrub encroachment (Anthelme *et al.*, 2001, Hiltbrunner *et al.*, 2014). Green alder (*Alnus viridis* [Chaix D.C]) is a main constituent of such tall shrublands and impedes further succession towards conifer forests (Tappeiner and Cernusca, 1989; Didier, 2001; Wohlfahrt *et al.*, 2003; Gehring-Fasel *et al.*, 2009) through its nitrogen fixing capacity (Hiltbrunner *et al.*, 2014). Recent remote-sensing studies have demonstrated strong increases in shrub abundance in arctic and alpine ecosystems (Sturm *et al.*, 2001; Tape *et al.*, 2006; Myers-Smith *et. al.*, 2011; Elmendorf *et al.,* 2012). This has led to a reduction in plant (Tasser and Tappeiner, 2002; Maurer *et al.*, 2006; Spiegelberger *et al.*, 2006) and animal diversity (e.g., Anthelme *et al.*, 2001; Marini *et al.*, 2009), but effects in terms of ecosystem functioning and the water balance in particular, have remained largely unexplored.

Because of their higher water consumption (evapotranspiration: ET), forested catchments often yield less runoff than grasslands (Bosch and Hewlett, 1982; Brown *et al.*, 2005; Farley *et al.*, 2005). Similarly, the growth of tall grass swards and dwarf shrub invasion can be expected to alter the water balance. For alpine grasslands it has been shown that ET may increase by up to 10% due to abandonment (Körner *et al.*, 1989) but effects can be larger for more vigorous grassland types (Inauen *et al.*, 2013). Conversely, some experiments have shown that abandonment may, at least temporarily, reduce ET due to the accumulation of dead plant material (Tappeiner and Cernusca, 1998; Rosset *et al.*, 2001).

High leaf area indices (LAI) are commonly associated with high ET rates (van den Bergh *et al.,* 2013; Obojes *et al.*, 2014). Canopy conductances for water vapour, and thus also ET, saturate at LAI values above 3 to 4 $m^2\ m^{-2}$ (Rosset *et al.*, 1997; Hammerle *et al.*, 2008; Van den Bergh *et al.*, 2013). Since LAI of alpine grasslands are commonly well below such saturation levels, (Cernusca and Seeber, 1981; Körner 2003; Inauen *et al.*, 2013), effects of abandonment on ET are expected to be more pronounced at montane elevations.

Globally, plant transpiration comprises *ca.* 70% of terrestrial ET (Jasechko *et al.*, 2013; Schlesinger and Jasechko, 2014) also for alpine grasslands (Körner 2003). For the Alps, precipitation exceeds ET by far, which is why they are an important source of water for the European lowlands (Weingartner *et al.,* 2007). If abandonment inceases ET, grazing cessation may reduce part of these benefits. While effects on the water balance may be most pronounced at montane sites, they may have larger economic consequences at higher (alpine) elevation, given the larger land area and the higher potential energy (higher falling heigth). These effects have to be viewed in the light of the 56 % of the Swiss and 16 % of the European electric energy production from mountain catchments; Swiss Federal Office for Energy (2012), Eurostat (2012). Hence, small abandonement effects in alpine terrain may translate into relatively large reductions in the hydro-electric potential.

Here we quantify effects of land use on ET and catchment hydro-electric potential across a 1000 m elevation gradient in the Swiss central Alps. We set-up a lysimeter based, manipulative experiment covering the major montane and alpine vegetation belts, upwards from 1500 m a.s.l. We hypothesize that abandonment leads to higher ET rates, particularly at montane elevations. Higher ET reduces deep seepage, catchment water yield and thus, hydro-electric potential. For alpine sites we expect smaller effects on the water balance per unit land area to be set off by larger land area and a higher potential energy.

Material and methods

To quantify the effects of elevation and land use on the water balance and hydro-electric potential of a catchment, we set-up a lysimeter experiment at three sites (two montane and one alpine), *ca.* 500 meters of elevation apart. The sites were located in the Ursern valley in the Swiss central Alps on more or less level terrain. The low site (L) (46°36'N, 8°32'E) and mid elevation sites (M) (46°35'N, 8°29'E) at 1490 and 1960 m a.s.l., had a mean peak season leaf canopy height of 15 to 20 cm. The high elevation site (H) at 2440 m a.s.l. (46°34'N, 8°25'E) had a mean peak season leaf canopy height of 5 to 10 cm (always disregarding inflorescences). Currently, the climatic treeline in this part of the central Alps lies between 2000 and 2100 m a.s.l.

Annual precipitation (measured at the nearby MeteoSwiss weather stations in 'Andermatt' at 1438 m a.s.l. and 'Gütsch ob Andermatt' at 2287 m a.s.l.) commonly ranges from 1500 to 1900 mm and is more or less equally distributed across the year (MeteoSwiss). ET in this region is generally not limited by soil moisture availability. During the experiment, weather conditions (air temperature and humidity, solar radiation and wind speed) were recorded at all three sites in 10 minute intervals at 1.5 to 1.8 m above the ground using automatic weather stations (Vantage Pro 2, Davis Instruments Corporation, Hayward, CA, USA).

To measure daytime ET rates and land use effects, we installed weighable, monolithic lysimeters at all sites (autumn 2008 at H, spring 2009 at L and M; for a detailed description see Inauen *et al.*, 2013 and van den Bergh *et al.*, 2013). Each weighable lysimeter consisted of an inner bucket (diameter 28 cm, depth 22 cm) with an intact soil-vegetation monolith and an outer bucket to ease lysimeter handling (diameter 29 cm, depth 32 cm). Monoliths were cut to tightly fit into the inner buckets (surface 1.5 to 2 cm below the bucket's rim in order to avoid lateral runoff) and positioned in the field such that the natural canopy aerodynamics remained undisturbed. At each site, monoliths were selected from three to four different vegetation types representative

for each site. 'Grass' lysimeters at L and M were dominated by *Poaceae* (e.g., species of *Poa*, *Deschampsia* and *Festuca*) and by *Cyperaceae* at H (*Carex curvula* [ALL.]). '*Nardus*' lysimeters were present at all three sites and were dominated by *Nardus stricta* (L.), a perennial bunch grass found across the entire elevational gradient. 'Herb' lysimeters consisted of a suite of herbaceous species such as *Asteraceae*, *Rosaceae* and *Fabaceae.* We installed 8 WLs of each of these vegetation types at L and M and 15 of each type at H (grassland types were more or less equally common at the three sites).

To establish more long-term hydrological consequences of abandonment and to quantify the effects of dwarf shrub establishment on ET at montane elevations, we installed 4 WLs at L and M with *Calluna vulgaris* (L.) and *Vaccinium* species (mainly *Vaccinium myrtillus* and *Vaccinium vitis-idaea*). At the high site, shrub invasion is uncommon. Instead, after prolonged periods of neglect, we see that tall grass species (e.g. *Agrostis schraderiana* [Bech] and *Deschampsia flexuosa* [L.] become dominant. We therefore installed 6 WLs with *Agrostis schraderiana* (Bech) at H. We installed additional WLs with vegetation characteristic for shallow (8 WLs; species: *Alchemilla spp., Arnica montana, Hieracium spp, Thymus vulgaris*, etc.) and wet soils (4 WLs; species mainly *Carex nigra* that is common in montane fens) to measure potential minimum and maximum daytime ET rates at L and M (*Carex nigra* monoliths were installed in unperforated buckets to guarantee permanent high soil moisture). In the following, these types will be referred to as 'grass', *Nardus*, 'herb', *Agrostis, Calluna*, *Vaccinium*, 'low herb' and *Carex*. We installed a total of 44 WLs at L and M, and 51 at H, yielding a total of 139 WLs. In the year 2009, 6 grass, *Nardus* and herb WLs were subjected to a free air CO_2 enrichment experiment at H, explaining the different numbers of replicates during that year (for results from the CO_2 enrichment experiment see Inauen *et al.*, 2013).

Weighable lysimeter evapotranspiration (WLET) was measured for single bright days (daytime hours only) in 2009 and 2010 by weighing lysimeters on an electrical balance (precision ± 0.1 g) placed in a wind free, on-site, shelter. From the weight difference

between morning (before local sunrise) and evening (after local sunset), we calculated daytime WLET. Bright day ET was measured after WL installation (spring 2009) from late summer 2009 until autumn 2010 at L and M whereas at H, WLET was measured since 2008 (2009- and 2010-data presented here). As we aim to investigate effects of land use and elevation, we only present data for bright days where WLET was measured for clipped and unclipped WLs at all sites. We use the word 'bright' to describe weather conditions during these rainless days but afternoon cloud formation is common in this region. During 2009 and 2010 WLET rates were measured for a total of 6 and 12 days at L, for 6 and 10 days at M and for 21 and 7 days at H. For these two years, concurrent WLET measurements were performed at all sites during 5 and 7 days, respectively.

Deep seepage collectors (DSCs) were installed by cutting undisturbed monoliths to fit stainless steel buckets with a bottom reservoir of approximately 5 L to collect seepage water (similar dimensions as WLs, for details see Van den Bergh *et al.*, 2013). DSCs were set up at H in summer 2006 and at L and M in spring 2009. At all sites, they were maintained and operated until autumn 2011. At each site, 8 grass, *Nardus* and herb DSCs were installed (10 herb DSCs at H). At L and M, we built 4 DSCs with *Calluna* and *Vaccinium* and at H we installed 8 DSCs with *Deschampsia* and *Agrostis*. L and M were fitted with 8 DSCs with low herb vegetation (we installed no *Carex* DSCs because they cannot be employed for permanently waterlogged soils). In total, we installed 122 DSCs at the three sites. ET rates from DSCs (DSCET) were calculated by solving the water balance equation (Eq. 1):

$$P = R + ET + \Delta S \qquad \text{Equation 1}$$

Where P stands for precipitation, R for total runoff (deep seepage; lateral runoff is prevented by the rim of the container), ET for evapotranspiration and ΔS for the difference in soil moisture content (all in mm). Differences in soil moisture content were assumed to be negligible for the time period between the beginning and the end of the sampling period. Since precipitation measurements at weather station height

(usually at 2 m) tend to underestimate true precipitation (Duchon and Essenberg, 2001), we used precipitation values from an additional tipping bucket rain gauge installed at 0.4 m above ground level (RAINEW, Rainwise Inc., Barharbor, ME, USA) to calculate ET rates for DSCs. Besides rainfall, a weather station recorded air temperature and humidity, solar radiation and wind speed at 10 minute intervals (Vantage Pro 2, Davis Instruments Corporation, Hayward, CA, USA).

To assess differences in ET between grazed and abandoned grassland, we simulated grazing by clipping the vegetation of WLs and DSCs. Dwarf shrubs and *Carex* remained unclipped as they are generally avoided by livestock. Grazing by sheep (common at alpine elevations) and cattle (more common at the two montane sites) is the dominant land use form in this region and typically reduces vegetation height to 3 to 4 cm (unclipped vegetation hence represented abandoned grassland). WLs and DSCs were clipped at peak biomass at the time when farmers commonly bring their animals to a site (WLs and DSC were clipped approximately at the same time, first at L, then at M and last at H). At all sites, the clipping treatment was repeated in order to maintain the grazing effect.

For DSCs, mean daily DSCET rates were calculated for the same period at all sites for both years ('whole season') and for the time period after clipping ('after clipping only'). 'Whole season' DSCET was calculated for sampling periods of 86 and 79 days for 2010 and 2011 respectively (DSCs were emptied 8 and 6 times). 'Post clipping' DSCET was calculated for different sampling periods at L, M and H (2010: 59, 59 and 31 days, DSCs were emptied 6, 6 and 3 times; 2011: 79, 61 and 47 sampling days, DSCs were emptied 6, 5 and 3 times).

At the end of the experiment, above-ground phytomass from all WLs and DSCs was clipped to the ground level, sorted into biomass, necromass (also live woody stems of dwarf shrubs) and cryptogams (mosses and lichens), dried (48 hours at 80 °C) and

weighed (final phytomass harvest of WLs took place in autumn 2010 and of DSCs in autumn 2011).

Catchment land cover assessment and quantification of abandonment responses

In order to scale land use effects to the total catchment area, we produced a high resolution land cover map. Vegetated and bare lands were distinguished using unsupervised maximum likelihood classification (ArcGIS; 100 similarity classes) on a composite Spot image from the summer of 2004/2005. Classes were then manually assigned to 'vegetated' or 'bare' using SWISSIMAGE orthophotos as a visual reference. Additional land cover types such as shrubland (mainly consisting of *Alnus viridis* [75-85%] and *Sorbus aucuparia* [15-25%] interspersed with *Salix* spp., *Betula pendula* and *Populus tremula*), conifer protection forests, hay meadows, permanent snow and glaciers, water bodies and settlements, were manually drawn from the orthophotos. All remaining vegetated land was assigned to the grassland class studied here. This class included dwarf shrubs as these cannot be distinguished from grassland on the photos. Dwarf shrub vegetation commonly consisted of *Calluna vulgaris* (L.) and different *Vaccinium* species on South facing slopes. Dwarf shrub vegetation on other slope aspects was more diverse with *Vaccinium* species, *Rhododendron ferrugineum*, *Empetrum nigrum* and *Arctostaphylos ursinum* (the latter two were less abundant). Land cover polygons were transformed into a grid with a resolution of 2 x 2 meters. For the delineation of the catchment we used the 'watershed' tool from ArcGIS and the swissALTI3D digital elevation model (Swisstopo; resolution: 2 x 2 m). True surface area was calculated using the 'surface area calculation tool' for ArcGIS from Jenness (2004).

The land cover map was divided into four elevational ranges (1400-1800, 1800-2200 and 2200-2600 and 2600+ m a.s.l.). Differences in ET between clipped and unclipped DSCs of the common vegetation types (grass, *Nardus* and herb) at L, M and H, were scaled to the 'grassland' and 'hay meadows' land cover classes within the three belts (only when the abandonment effect was statistically significant; and hay meadows were only

present in the lowest elevational range; for grassland above 2600 m a.s.l. we assumed no abandonment effects). At L and M, ET rates were similar for dry and clipped vegetation (see results section). We estimated that 10 % of the grasslands in the low and mid elevation range, were occupied by sparse grassland typesEffects of abandonment on the catchment hydro-electric potential were quantified by calculating the loss in potential energy resulting from reduced runoff (increased ET means equally reduced runoff). To calculate the inherent potential energy of water we used the average elevation for the three elevational belts as falling height (1600, 2000 and 2400 m a.s.l.). Further, we assumed an 85% conversion efficiency of hydro-electric power plants and an average price per kWh of 0.09 CHF (at the time of the writing of this paper 1 CHF equalled 0.92 EUR)

Statistical analyses

Calculations and statistical analyses were performed using the open-source software R, version 2.15.2 (R Development Core Team, 2010). For testing the significance of elevation, grassland type (grassland types nested within sites), clipping treatment and date on WLET rates, we used linear mixed effect models from the *nlme* package (tested for data of both years separately; Pinheiro *et al.*, 2011). We used likelihood ratio tests to find the optimal random effects and variance structure (fit using restricted maximum likelihood; REML). Hereafter, we determined the minimal adequate model by comparing the full model to a reduced model, i.e. testing whether deleting fixed effects reduced the explanatory power of the model. We used Tukey's HSD test for comparing group means from the *multcomp* package (Hothorn *et al.*, 2008). Normality and homogeneity of variances of the residuals for mixed models were assessed visually (log or power transformations were applied when necessary). For the analysis of DSCET and phytomass data, we used analysis of variance or non-parametric tests in cases where normality and/or variance homogeneity could not be achieved by data transformation (necromass; lichens and moss data). P-values <0.05 were considered statistically significant.

Results

Bright day weather conditions

During our WLET measurements in 2009 and 2010, mean solar radiation was similar across the sites (Tab. 1). Mean day time air temperature decreased with elevation at lapse rates of 2.1 and 4.1 K km^{-1} from L to M, and of 7.6 and 6.7 K km^{-1} from M to H in 2009 and 2010. Vapour pressure deficit declined with elevation for both years (L to M 2009/2010: -0.12/-0.10 kPa km^{-1}; M to H 2009/2010: -0.29/-0.03 kPa km^{-1}).

Table 1. Bright day daytime weather conditions (mean ± sd) for 2009 and 2010 WLET measuring days (5 and 7 sampling days; daytime corresponds to the time between local sunrise to local sunset) at L, M and H. Note that standard deviations reflect variability rather than error.

Site (elevation m a.s.l.)	Year	Air temperature (°C)	Wind speed (m s^{-1})	Solar radiation (MJ d^{-1})	VPD (kPa)
L (1490)	2009	14.6 ± 2.2	2.3 ± 0.5	20.1 ± 2.1	0.61 ± 0.19
	2010	15.6 ± 2.4	2.0 ± 0.2	20.8 ± 4.3	0.55 ± 0.23
M (1960)	2009	13.6 ± 1.4	2.3 ± 0.8	21.6 ± 1.8	0.56 ± 0.13
	2010	13.7 ± 2.3	2.1 ± 1.1	20.8 ± 4.6	0.51 ± 0.22
H (2440)	2009	10.0 ± 1.0	2.1 ± 0.3	20.9 ± 1.6	0.42 ± 0.11
	2010	10.5 ± 1.9	3.5 ± 1.0	22.6 ± 3.8	0.49 ± 0.14

Weather conditions during DSCET measurements

When discussing DSCET measurements we distinguish ‘whole season’ and ‘post clipping measurements. To allow comparisons across elevations, 'whole season' data cover the same sampling period across the three sites and included days from before as well as after the clipping treatment, a conservative approach in light of the truncation of the longer early and late season at lower elevation. Also the 'after clipping' sampling period was shorter at higher elevation. Since, actual season length

differed among sites, such comparisons cannot be done for the entire growing period, also because this would incur different weather situations.

Because, in contrast to weighing lysimeters, 'whole season' DSCET measurements were performed during bright as well as rainy days), mean air temperature, solar radiation and vapour pressure deficit were lower for these data than for the bright days at which WLET was measured. In 2010 and 2011, air temperature decreased with elevation (L to M 2010/2011: -5.4/-5.4 K km^{-1}; M to H 2010/2011: -7.0 K/-6.0 K km^{-1}; see Table 5 in Chapter 2), and solar radiation was similar across sites for the same period of time (L 2010/2011: 19.0/19.4 MJ d^{-1}; M 2010/2011: 18.9/19.5 MJ d^{-1}; H 2010/2011: 18.4/19.2 MJ d^{-1}). Differences in vapour pressure deficit were largest between L and M and smaller between M and H (L 2010/2011: 0.47/0.47 kPa; M 2010/2011: 0.35/0.37 kPa; H 2010/2011: 0.30/0.33 kPa). In 2010, rainfall was highest at H (497 mm), and lower at M (371 mm) and L (360 mm) whereas in 2011, rainfall was highest at M (418 mm) and lower at H (397 mm) and L (311 mm).

Effects of abandonment on bright day evapotranspiration (WLET)

In line with our expectations, abandonment led to higher WLET rates and this effect decreased with elevation. Analysis by linear mixed effects models revealed that differences in WLET were largely explained by clipping, day of the year (DOY) and elevation (here synonymous with site), while grassland type added little to the explanatory power of the models (only statistically significant in 2010, Table 2). A significant clipping x site interaction indicated that abandonment led to pronounced increases in WLET at L and M, but not at H (across all 21 bright days in 2009, and tested for each vegetation type separately, abandonment led to significantly higher WLET rates in *Agrostis* [+26%] and *Nardus* [+10%], but not in mixed grass [+5%] and herb [+3%]). During both years, WLET decreased with DOY (days getting shorter after June) and this trend was most pronounced at H likely because there, cooler weather was associated with more clouds and fog. For both years, we found a significant

interaction between grassland type and DOY on ET effects, indicating that the temporal decline in WLET, differed across grassland types.

Table 2. The effects of site (L, M, H), treatment (abandonment), day of year (DOY) grassland type (GT; nested within sites) and their interactions on the WLET rates in 2009 and 2010 (5 and 7 days at all sites after the application of the clipping treatment). Analysed by two linear mixed effect models (model fitted to WLET rates obtained from grass, *Nardus* and herb, unsignificant variables were removed from the model).

Year	factor	df	F-value	P-value
2009	site	2	30.2	**<0.001**
	treatment	1	111.2	**<0.001**
	DOY	1	29.8	**<0.001**
	GT(site)	6	2.0	0.068
	site x treatment	2	24.9	**<0.001**
	site x DOY	2	3.1	**0.047**
	treatment x DOY	1	5.2	**0.024**
	GT(site) x DOY	6	3.6	**0.002**
	GT(site) x treatment	6	1.8	0.097
2010	site	2	113.7	**<0.001**
	treatment	1	24.4	**<0.001**
	DOY	1	7.2	**<0.001**
	GT(site)	6	3.5	**0.002**
	site x treatment	2	8.7	**<0.001**
	site x DOY	2	22.0	**<0.001**
	treatment x DOY	1	23.9	**<0.001**
	GT(site) x DOY	6	2.6	**0.015**

Hence, WLET rates were mostly determined by elevation and the clipping treatment (biomass). Grassland type, albeit being a significant factor, was less important.

Because we are mainly interested in land use effects and how these evolve over time (succession) and as grazing affects grasslands as a whole and not for separate grassland types, we focus on immediate (clipped vs unclipped) and more long term (invasion by dwarf shrubs and *Agrostis* and *Deschampsia*) impacts of the clipping treatment. When swards behave fundamentally different, we will refer to individual grassland types.

Across the common grassland types at L (mixed grass, *Nardus* and herb), WLET increased in response to abandonment by 30 and 15 % in 2009 and 2010 (Fig. 1; WLET data for individual grassland types can be found in Table 3). For the same years, at M, WLET increased by 37 and 24%. At H, we found smaller abandonment effects as WLET increased, on average by 6 and 3% only. At M, WLET from dwarf shrubs (*Calluna* and *Vaccinium)* was higher compared to grazed grassland but lower when compared to abandoned grass turfs. At H, WLET of *Agrostis* exceeded that of the other clipped grassland types by 21 and 27% (note: Fig. 1 compares WLET rates across the common clipped grassland types to those from unclipped *Agrostis*; Table S1 compares WLET rates from clipped and unclipped *Agrostis*). At L and M, WLET rates in the small stature herbaceous vegetation were similar to those of clipped swards while rates from wet *Carex* swards were similar to unclipped grassland.

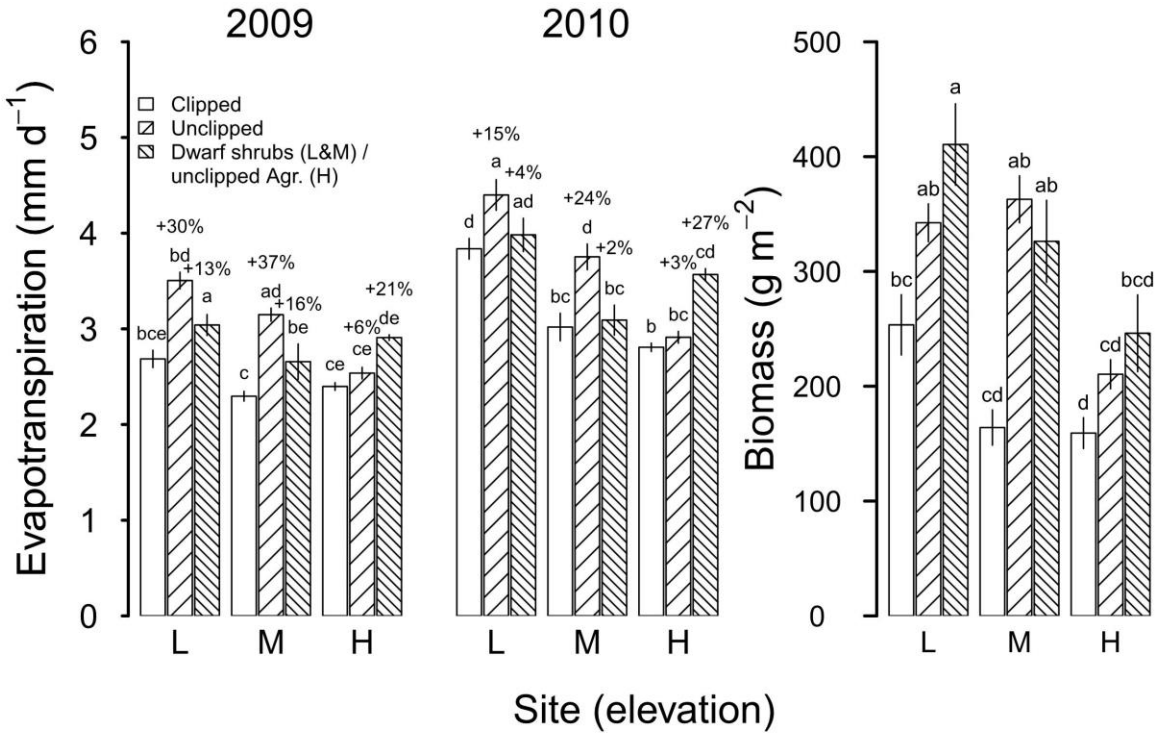

Figure 1. Mean daytime bright day WLET (means ± se) and biomass of clipped and unclipped grassland (all common grassland types combined) and dwarf shrubs at L, M and H for the growing seasons of 2009 and 2010 (note: *Calluna* and *Vaccinium* at L and M; late successional grassland of *Agrostis* at H). Different letters indicate significant differences at $p<0.05$ (within years, across sites).

Table 3. Daytime WLET rates (mean ± sd) and unclipped to clipped WLET ratios ($WLET_{uc}/WLET_c$) of different vegetation types at L, M and H in 2009 and 2010 (5 and 7 sampling days in 2009 and 2010 at all sites). Different letters indicate significant differences in WLET within sites for years separately (see mixed models in Table 2; significant at $p<0.05$). The number of replicates is given in brackets.

Site	Vegetation type	WLET 2009 clipped mm d^{-1}	WLET 2009 unclipped mm d^{-1}	WLET 2010 clipped mm d^{-1}	WLET 2010 unclipped mm d^{-1}	$WLET_{uc}/WLET_c$ 2009	$WLET_{uc}/WLET_c$ 2010
L	grass	2.5 ± 0.3^{a}(4)	3.4 ± 0.4^{b} (4)	3.8 ± 0.6^{ab} (4)	4.6 ± 0.5^{b} (4)	1.35	1.21
	Nardus	2.5 ± 0.2^{a} (4)	3.6 ± 0.1^{b} (4)	3.7 ± 0.2^{ab} (4)	3.9 ± 0.5^{ab} (4)	1.45	1.04
	herb	3.0 ± 0.3^{ab} (4)	3.4 ± 0.4^{b} (4)	4.0 ± 0.3^{ab} (4)	4.7 ± 0.4^{b} (4)	1.14	1.18
	Calluna		3.3 ± 0.2^{ab} (4)		4.3± 0.4^{ab} (4)		
	Vaccinium		2.8 ± 0.3^{ab} (4)		3.7 ± 0.4^{ab} (4)		
	low herb		3.1 ± 0.2^{ab} (8)		3.6 ± 0.5^{a} (8)		
	Carex		*n.a.*		4.8 ± 1.0^{b} (4)		
M	grass	2.2 ± 0.1^{bc}(4)	3.3 ± 0.2^{a} (4)	3.2 ± 0.8^{acd} (4)	3.8 ± 0.4^{bc} (4)	1.47	1.18
	Nardus	2.3 ± 0.2^{bc}(4)	2.9 ± 0.2^{ab} (4)	2.9 ± 0.2^{cd} (4)	3.3 ± 0.2^{bd} (4)	1.30	1.16
	herb	2.4 ± 0.2^{bc}(4)	3.2 ± 0.1^{a} (4)	3.0 ± 0.3^{cd} (4)	4.2 ± 0.3^{b} (4)	1.35	1.39
	Calluna		2.6 ± 0.4^{ac} (4)		3.1 ± 0.2^{cd} (4)		
	Vaccinium		2.7 ± 0.7^{ac} (4)		3.1 ± 0.6^{cd} (4)		
	low herb		2.3 ± 0.2^{c} (8)		3.0 ± 0.2^{d} (8)		
	Carex		3.2 ± 0.5^{a} (4)		4.0 ± 0.2^{ab} (4)		
H	grass	2.3 ± 0.1^{a} (3)	2.5 ± 0.3^{ab} (6)	2.9 ± 0.1^{b} (7)	2.9 ± 0.3^{b} (8)	1.08	1.03
	Nardus	2.4 ± 0.1^{ab} (3)	2.5 ± 0.4^{ab} (6)	2.7 ± 0.2^{b} (7)	2.8 ± 0.3^{b} (8)	1.05	1.05
	herb	2.5 ± 0.1^{ab} (3)	2.6 ± 0.1^{ab} (6)	2.9 ± 0.2^{b} (7)	3.0 ± 0.2^{b} (8)	1.05	1.03
	Agrostis	2.5 ± 0.1^{ab} (3)	2.9 ± 0.1^{b} (3)	2.9 ± 0.3^{b} (3)	3.6 ± 0.1^{a} (3)	1.14#	1.23

At H, WLET rates were measured for a total of 22 sampling days in 2009. Across all these days, $WLET_{uc}/WLET_c$ was 1.26.

'Whole season' and 'post clipping' abandonment responses (DSCET)

'Whole season' DSCET declined with increasing elevation during both years (Table 4). In 2010, abandonment (treatment) had a marginally significant effect on DSCET but there was a statistically significant interaction between site and treatment, indicating that the effect of abandonment was depending on elevation (significant at L). Grassland type significantly influenced DSCET, due to high transpiration from grass dominated swards. In 2011, 'whole season' DSCET again decreased with elevation. In this year, abandonment led to significantly higher DSCET, again at L only. Grassland type and interactions between grassland type and other factors did not affect DSCET.

Table 4. Minimum adequate models specifying the effects of site, treatment (abandonment), grassland type (GT; nested within sites; grassland types included: *Agrostis, Deschampsia*, grass, herb, *Nardus, Calluna, Vaccinium*) and their interactions on 'whole season' DSCET for 2010 and 2011 (non-significant variables were removed from the model).

Year	factor	df	F-value	P-value
2010	site	2	291.7	**<0.001**
	treatment	1	3.8	0.055
	GT(site)	14	3.1	**<0.001**
	treatment x site	2	3.5	**0.035**
2011	site	2	20.6	**<0.001**
	treatment	1	19.0	**<0.001**

At L in 2010, 'post clipping' DSCET was not significantly different for grazed and abandoned swards nor for dwarf shrubs ($F_{(2, 29)}$=1.8, p=0.18). Still, unclipped DSCs showed 9% (18 mm) higher ET rates than clipped DSCs (Fig. 2; for grassland type specific data see Table 5). In dwarf shrubs, 'post clipping' DSCET exceeded ET from grazed swards by only 2% or 5 mm. Abandonment led to higher DSCET rates in grass dominated swards only (+27%; Table 5) and not in herb and *Nardus* (-3 and +5%). Hence, the abandonment and the abandonment x grassland type factors were significant ($F_{(1, 24)}$=5.0, p=0.036; $F_{(2, 24)}$=4.3, p=0.025). In 2011 DSCET from abandoned swards and dwarf shrubs was 27 and 13% or 54 and 27 mm higher than in clipped grassland. 'Post clipping' DSCET rates were significantly different for clipped and unclipped grassland and dwarf shrubs ($F_{(2, 29)}$=15.0, p<0.001). For this year, the effect of abandonment was similar across grassland types (+34, +28 and +18% for grass, herb and *Nardus* respectively; grassland type did not affect 'post clipping' DSCET rates). At the mid elevation site in 2010, 'post clipping' DSCET rates were similar for clipped and unclipped swards and dwarf shrubs (+16 and +24% or +14 and +20 mm for unclipped turfs and dwarf shrubs in comparison to clipped swards). In grass dominated swards we measured a 41% increase in unclipped 'post clipping' DSCET but due to high

variability in rates, this difference was not significant. Also in 2011, DSCET rates were similar for the common grassland types (clipped and unclipped) and dwarf shrubs. At H in 2010, 'post clipping' DSCET rates in common, abandoned grassland types were 24% lower compared to clipped swards (-19mm). Invasion by *Agrostis* and *Deschampsia* also led to lower DSCET after clipping (-32% or 25 mm). This difference between clipped and abandoned and clipped and tall, late successional grasses was highly significant ($F_{(2, 30)}$=26.0, p<0.001). By contrast, in 2011, 'post clipping' DSCET rates of clipped, unclipped and tall grasses were not significantly different (+6 and -5 mm for unclipped and unclipped tall swards respectively).

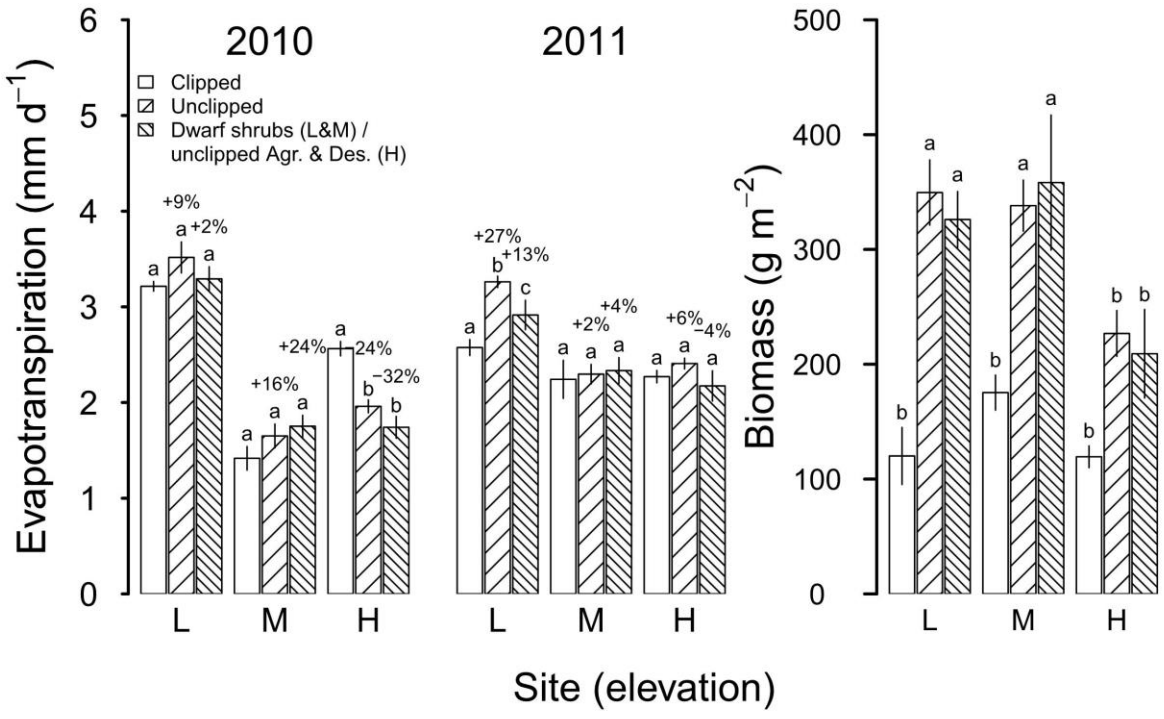

Figure 2. Mean daily 'post clipping' DSCET rates for 2010 and 2011 and biomass of clipped and unclipped grassland (common grassland types combined) and dwarf shrubs at L, M and H (dwarf shrubs at L and M, *Agrostis* and *Deschampsia* at H). Different letters indicate significant differences at p<0.05 (within years, across sites).

Table 5. Mean daily 'post clipping' DSCET (mean ± sd) in 2010 and 2011, clipped to unclipped DSCET ratios ($DSCET_{uc}/DSCET_c$) and unclipped minus clipped DSCET for the post clipping sampling period (ΔDSCET, sp = sampling period) for all vegetation types at L, M and H. Significant differences in DSCET are indicated by different letter (tested within sites and within years). The number of replicates is given in brackets with DSCET rates.

Site	Vegetation type	DSCET				$\frac{DSCET_{uc}}{DSCET_c}$		ΔDSCET	
		2010		2011		2010	2011	2010	2011
		clipped mm d^{-1}	unclipped mm d^{-1}	clipped mm d^{-1}	unclipped mm d^{-1}			mm sp^{-1}	mm sp^{-1}
L	grass	3.2 ± 0.1^{b} (4)	4.0 ± 0.4^{a} (4)	2.4 ± 0.3^{b} (4)	3.3 ± 0.2^{a} (4)	1.27	1.34	50	66
	Nardus	3.3 ± 0.2^{ab} (4)	3.5 ± 0.3^{ab} (4)	2.7 ± 0.2^{ab} (4)	3.2 ± 0.2^{a} (4)	1.05	1.18	9	39
	herb	3.1 ± 0.2^{b} (4)	3.0 ± 0.5^{b} (4)	2.6 ± 0.4^{ab} (4)	3.3 ± 0.2^{a} (4)	0.97	1.28	-5	58
	Calluna		3.4 ± 0.3^{ab} (4)		2.8 ± 0.5^{ab} (4)				
	Vaccinium		3.2 ± 0.4^{ab} (4)		3.0 ± 0.4^{ab} (4)				
	dry herb		3.0 ± 0.5^{b} (8)		2.7 ± 0.4^{ab} (8)				
M	grass	1.4 ± 0.5^{a} (3)	2.0 ± 0.3^{a} (4)	2.2 ± 0.2^{a} (3)	2.3 ± 0.3^{a} (4)	1.41	1.06	34	8
	Nardus	1.6 ± 0.5^{a} (4)	1.6 ± 0.4^{a} (4)	2.6 ± 1.0^{a} (4)	2.5 ± 0.4^{a} (4)	1.02	0.95	1	-9
	herb	1.3 ± 0.2^{a} (4)	1.3 ± 0.4^{a} (3)	1.9 ± 0.3^{a} (4)	2.1 ± 0.4^{a} (4)	1.02	1.10	1	11
	Calluna		1.7 ± 0.2^{a} (4)		2.4 ± 0.5^{a} (4)				
	Vaccinium		1.8 ± 0.5^{a} (4)		2.2 ± 0.5^{a} (4)				
	Dry herb		1.8 ± 0.6^{a} (7)		2.7 ± 0.6^{a} (8)				
H	grass	2.5 ± 0.2^{ab} (4)	2.1 ± 0.4^{abc} (3)	2.2 ± 0.3^{a} (3)	2.4 ± 0.1^{a} (3)	0.84	1.08	-13	8
	Nardus	2.5 ± 0.2^{ab} (4)	1.9 ± 0.2^{bc} (4)	2.2 ± 0.2^{a} (4)	2.5 ± 0.3^{a} (4)	0.75	1.11	-20	12
	herb	2.7 ± 0.4^{a} (4)	2.0 ± 0.2^{bc} (6)	2.4 ± 0.2^{a} (4)	2.4 ± 0.2^{a} (6)	0.73	0.99	-23	-1
	Agrostis	2.1 ± 0.3^{abc} (4)	1.8 ± 0.2^{c} (4)	2.1 ± 0.1^{a} (4)	1.9 ± 0.5^{a} (4)	0.84	0.94	-11	-6
	Deschampsia	2.2 ± 0.4^{abc} (4)	1.7 ± 0.5^{c} (4)	2.2 ± 0.1^{a} (4)	2.4 ± 0.3^{a} (4)	0.78	1.11	-15	11

Biomass data

Biomass was similar in WLs and DSCs and was significantly lower at H in comparison to both L and M (Fig. 1, Fig. 2; for grassland type specific data see Table 7, 7). WL biomass from the three common unclipped grassland types was 1.5, 2.1 and 1.4 times larger than biomass of clipped swards at L, M and H, respectively (differences were largest in grass dominated lysimeters at L and M and in *Agrostis* at H). For DSCs these values were 3.1, 2.2 and 1.6 (the largest differences were observed in *Nardus*, herb and *Agrostis* dominated swards at L, M and H respectively). Cryptogams were abundant at H and uncommon or completely absent at L and M.

Table 6. Phytomass in WLs: biomass, necromass and cryptogam mass (g m^{-2}; mean ± sd; n between brackets with biomass data) at L, M and H. Different letters indicate significant differences between vegetation types (clipped and unclipped) within sites at $p < 0.05$.

		Biomass		Necromass		Cryptogams	
Site	Vegetation type	clipped (g m^{-2})	unclipped (g m^{-2})	clipped (g m^{-2})	unclipped (g m^{-2})	clipped (g m^{-2})	unclipped (g m^{-2})
L	grass	215 ± 64^{a}(4)	339 ± 72^{a} (4)	108 ± 92^{b}	95 ± 67^{b}	0 ± 0	0 ± 0
	Nardus	311 ± 117^{a}(4)	354 ± 13^{a} (3)	266 ± 216^{ab}	72 ± 21^{b}	0 ± 0	0 ± 0
	herb	229 ± 28^{a}(3)	338 ± 68^{a} (4)	196 ± 40^{ab}	215 ± 43^{ab}	0 ± 0	0 ± 0
	Calluna		390 ± 116^{a} (4)		598 ± 273^{a}#		0 ± 0
	Vaccinium		431 ± 95^{a} (4)		600 ± 93^{a}#		0 ± 0
	low herb		280 ± 89^{a} (4)		81 ± 73^{b}		4 ± 7
	Carex		421 ± 148^{a} (4)		205 ± 54^{ab}		0 ± 0
M	grass	147 ± 67^{b}(4)	369 ± 71^{a} (4)	107 ± 72^{b}	85± 80^{b}	0 ± 1	2 ± 2
	Nardus	177 ± 61^{b}(4)	361 ± 93^{a} (4)	183 ± 168^{b}	130 ± 186^{b}	3 ± 6	7 ± 13
	herb	168 ± 41^{b}(4)	359 ± 69^{a} (4)	245 ± 62^{b}	274 ± 60^{b}	0 ± 0	0 ± 0
	Calluna		283 ± 50^{ab} (4)		520 ± 120^{a}#		0 ± 0
	Vaccinium		370 ± 128^{a} (4)		217 ± 52^{b}#		1 ± 1
	low herb		344 ± 37^{a} (4)		75 ± 61^{b}		1 ± 2
	Carex		270 ± 27^{ab} (4)		244 ±35^{b}		0 ± 0
H	grass	108 ± 25^{b}(7)	175 ± 50^{ab}(8)	141 ± 61^{abc}	143 ± 55^{abc}	88 ± 30^{ab}	116 ± 97^{ab}
	Nardus	172 ± 64^{ab}(7)	245 ± 60^{a}(8)	239 ± 66^{ab}	263 ± 118^{a}	84 ± 39^{ab}	49 ± 84^{b}
	herb	197 ± 55^{ab}(7)	212 ± 62^{ab}(8)	106 ± 22^{c}	149 ± 43^{abc}	56 ± 48^{b}	129 ± 64^{ab}
	Agrostis	112 ± 32^{b}(3)	246 ± 58^{a}(3)	112 ± 32^{bc}	246 ± 58^{a}	112 ± 32^{ab}	246 ± 58^{a}

Woody, hence the high necromass

Table 7. Phytomass in DSCs: biomass, necromass and cryptogams (g m^{-2}; mean ± sd; n between brackets with biomass data) at L, M and H. Different letters indicate significant differences within sites at $p<0.05$.

		Biomass		Necromass		Cryptogams	
Site	Vegetation type	clipped (g m^{-2})	unclipped (g m^{-2})	clipped (g m^{-2})	unclipped (g m^{-2})	clipped (g m^{-2})	unclipped (g m^{-2})
L	grass	81 ± 33^{c}(4)	363 ± 70^{ab}(4)	404 ± 88^{a}	452 ± 92^{a}	0 ± 0^{a}	3 ± 1^{a}
	Nardus	203 ± 94^{bc}(4)	423 ± 132^{a}(4)	643 ± 51^{a}	572 ± 149^{a}	11 ± 12^{a}	7 ± 7^{a}
	herb	73 ± 60^{c}(4)	433 ± 25^{a}(4)	326 ± 40^{a}	348 ± 16^{a}	5 ± 7^{a}	13 ± 17^{a}
	Calluna		429 ± 173^{ab}(4)		574 ± 231^{a}		1 ± 2^{a}
	Vaccinium		287 ± 82^{ab}(4)		530 ± 304^{a}		1 ± 2^{a}
	low herb		213 ± 45 ^{a}(8)		263 ± 69		5 ± 6
M	grass	212 ± 70^{bc}(4)	442 ± 49^{a}(4)	236 ± 98^{b}	295 ± 46^{b}	30 ± 15^{a}	17 ± 19^{a}
	Nardus	167 ± 37^{c}(4)	361 ± 49^{ab}(4)	383 ± 119^{ab}	375 ± 98^{ab}	37 ± 30^{a}	31 ± 27^{a}
	herb	147 ± 32^{c}(4)	368 ± 36^{ab}(4)	276 ± 68^{b}	226 ± 59^{b}	11±11^{a}	1 ± 1^{a}
	Calluna		305 ± 59^{a}(3)		642 ± 55^{a}		0 ± 0^{a}
	Vaccinium		347 ± 81^{abc}(3)		790 ± 310^{a}		0 ± 0^{a}
	low herb		234 ±45 ^{ab}(8)		138 ±78		12 ± 18
H	grass	115 ± 57^{bc}(4)	182 ± 55^{ab}(4)	262 ± 28^{abc}	204 ± 91^{bc}	186 ± 58^{a}	243 ± 230^{a}
	Nardus	161 ± 10^{abc}(4)	273 ± 60^{a}(4)	360 ± 75^{ab}	393 ± 75^{a}	33 ± 17^{a}	22 ± 9^{a}
	herb	128 ± 46^{bc}(4)	226 ± 74^{ab}(4)	246 ± 24^{abc}	268 ± 56^{abc}	88 ± 93^{a}	59 ± 63^{a}
	Agrostis	75 ± 16^{c}(4)	136 ± 41^{bc}(4)	141 ± 44^{c}	178 ± 10^{c}	39 ± 29^{a}	50 ± 61^{a}
	Deschampsia	194 ± 7^{abc} (2)	184 ± 87^{a} (3)	219 ± 49^{ab}	400 ± 189^{a}	18 ± 19^{a}	46 ± 31^{a}

Up-scaling land use effects from DSCs to the catchment

An increase in ET reduces deep seepage and catchment runoff by the same amount. Higher ET thus diminishes a catchment's hydro-electric potential. Our land use experiment showed mixed abandonment effects. Inauen *et al.,* (2013), in a similar land use experiment at the high site (albeit with higher replication), have shown consistently higher DSCET rates in abandoned compared to clipped grassland. In these experiments, DSCET increased significantly in *Agrostis* and *Nardus* swards in 2008 and 2009 while in 2010 it was only higher in unclipped *Agrostis* swards. Different growing season weather during these experiments likely explain different abandonment responses across years at this highest site. The 2009 'post clipping' sampling period was warm and dry (29 days with more than 21 MJ of solar radiation; 21 MJ corresponds to the mean solar radiation measured during bright days in the WLET experiment) while the 2010 and 2011 sampling periods were more humid and cloudy (2010: 15, 15 and 8 bright days at L, M and H respectively; 2011: 33, 24 and 17 days with more than 21 MJ of solar radiation). 'Post clipping' sampling periods with many warm and dry days can be expected to show large abandonment effects (large absolute difference in ET between clipped and abandoned swards). Conversely, for years with few bright days, abandonment will have limited effects on a catchments water balance. The observed significant reductions of the abandonment effect on ET in 2010 at H may have resulted from less bright weather conditions and the fact that the vegetation surrounding the DSCs was lower compared to inside the instruments (due to trampling). At L and M, the vegetation in and outside the DSCs was more similar and buckets were hardly discernible in the field. This may have led to higher incoming rainfall in unclipped DSCs at H and hence an underestimation of DSCET (higher interception of rainfall). Negative abandonment effects at H in 2010 were thus likely the result of particularities in weather conditions and the instrument set-up rather than a decrease in ET itself.

To quantify changes in catchment runoff as associated with grazing cessation, we scaled the obtained mean differences in ET between clipped and abandoned DSCs to the distinguished elevational belts (only significant differences across the common grassland types were scaled; differences in runoff from L, M and H were scaled to all grassland between 1400 – 1800, 1800 – 2200 and 2200 – 2600 m a.s.l.; above 2600 we assumed no abandonment effects; because significant effects for 2010 at H were likely an artefact, they were not scaled to the 2200 – 2600 elevational belt).

The Reuss catchment expands from the valley bottom at 1440 m to the highest summits at 3590 m a.s.l. and covers 227 km² (true surface area). More than two thirds (70%) of the catchment is alpine terrain and lies above the current natural treeline. Grasslands (pastures and hay meadows) are the most prominent land cover type and make up 63% of the total catchment surface area (Fig. 3, 4). Pastures are much more common (61% of the catchment surface area) than hay meadows which occur primarily at the valley bottom (2% of the catchment surface). Shrubland represents 7% of the catchment area while conifer forests (protection forests above the villages and settlements) occupy less than 1% of the catchment. Permanent snow fields and glaciers currently make-up 4% of the catchment. The low mid and high elevation belts cover 28, 59 and 94 km² (we assumed no land use signals for elevations beyond 2600 m a.s.l.; these elevations cover 46 km²). Within these belts, grassland covered 61, 84 and 71% of the surface area respectively (17, 50 and 66 km²).

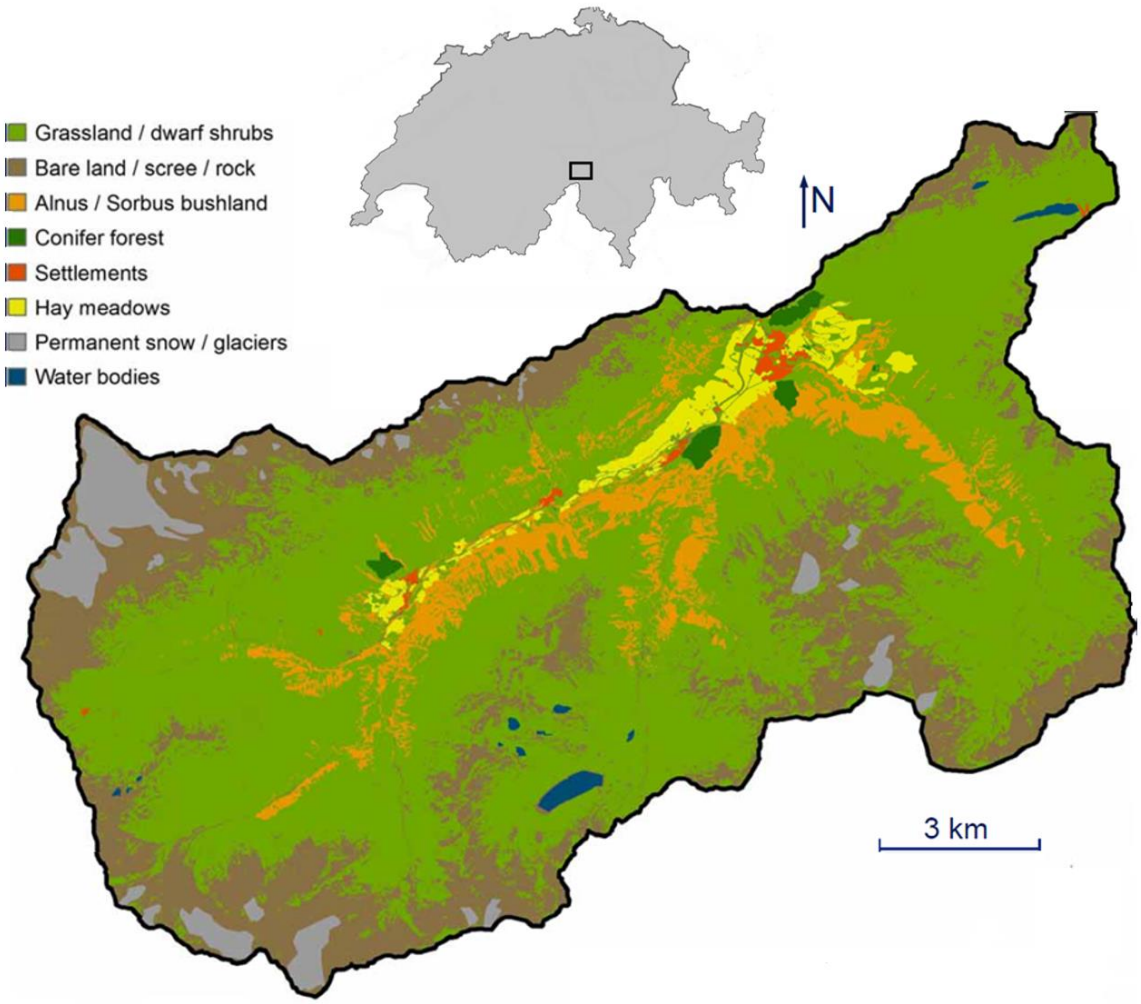

Fig. 3. Land cover map of the Ursern valley; in insert the location of the Ursern valley in Switzerland.

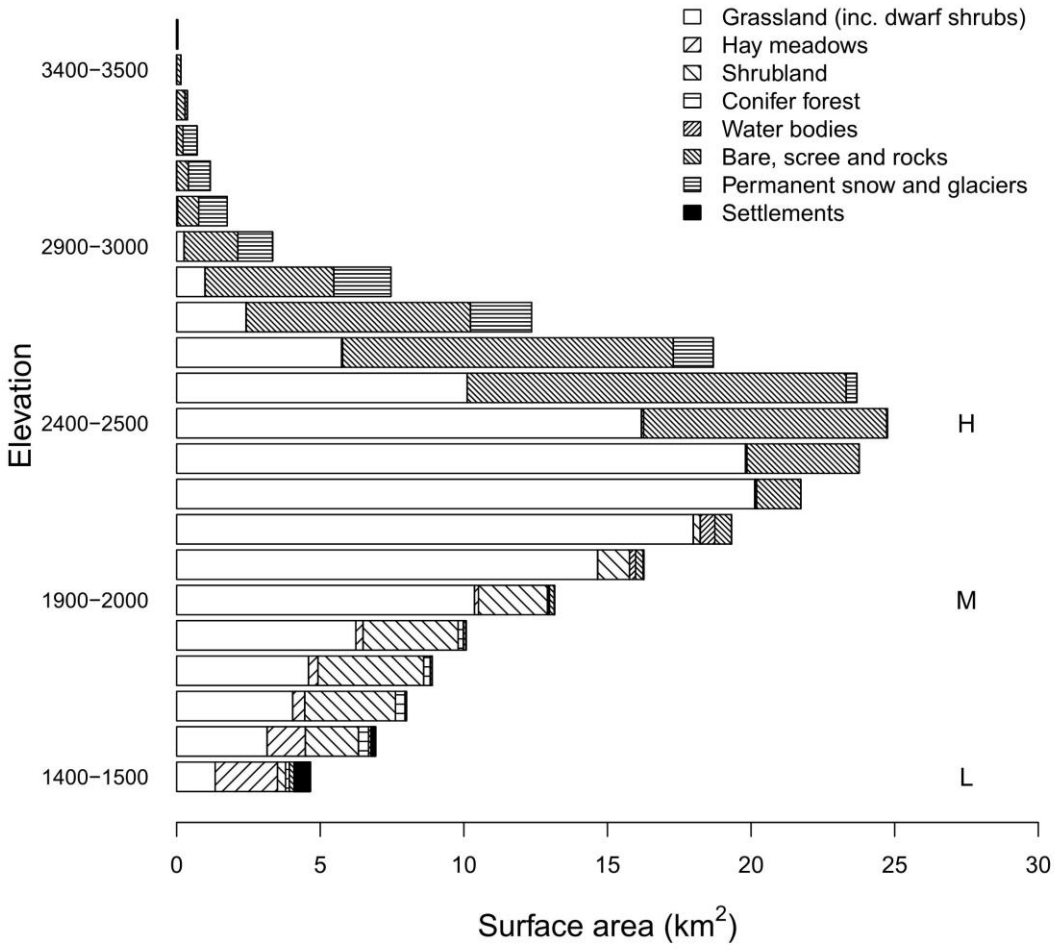

Figure 4. Elevational distribution of the eight different land cover classes in the Upper Reuss catchment (true surface area; total catchment area: 227 km²), based on Spot images and orthophotos of 2004/2005.The three experimental sites are indicated by L, M and H (right side of the figure).

We calculated effects of abandonment on runoff and the hydro-electric potential for elevational belts as a whole and per unit of land area (ha). The two years covered in our survey were rather humid, particularly when compared to 2009, one of the years reported on in the study by Inauen et al. (2013). Their effects were significant, our results went in the same direction, but were not always statistically significant also because of lower replication. Therefore, to establish the range by which abandonment

could reduce the hydro-electric potential of the Ursern valley, we used data of this study in conjunction with numbers reported by Inauen and co-workers. In this latter study it was reported that at H, DSCET in *Agrostis* increased by 74 mm a^{-1} (weather conditions were characterised as dry). During the other, years (2008/2010), increases in *Agrostis* DSCET were smaller and reached 30 mm. For all grassland types combined it was found that DSCET increased by 22 mm a^{-1} for 2008 and 2010 while again 2009 effects were larger and reached 35 mm a^{-1}. Because, in terms of leaf area, *Agrostis* is similar to grassland types found at L and M, effects reported for 2009 were assumed representative for warm and dry summers for the two montane belts.

Abandonment causes runoff to decline for the low belt irrespective of weather conditions but variability is large (18 to 74 mm; Table 8). At M, abandonment effects can be absent but also large during a warm and dry summer (0 to 74 mm). For the alpine belt, reductions in runoff are more modest and can be absent for a rainy summer but significant for a good weather scenario (0 to 35 mm). For the low elevation belt, cessation of land use reduces the hydro-electric potential of the low belt by 0.1 to 0.4 Mio CHF. For the mid elevation belt this reduction equals 0 to 1.4 Mio CHF and for the high belt 0 to 1.2 Mio CHF. Expressed per ha, we find that continued land use brings in guaranteed water savings for the low belt at 33 to 135 CHF ha^{-1}. At the mid elevation site this effect is potentially much larger due to greater falling height and ranges from 0 to 235 CHF ha^{-1}. At the high site, effects per ha tend to be smaller as elevation only partially counters smaller abandonment effects: here abandonment costs range from 0 to 125 CHF ha^{-1}. For the valley as a whole we find that land use adds between 0.1 to 2.9 Mio CHF (0.1 to 2.7 Mio EUR).

Table 8. Effects of abandonment on catchment runoff (reduction in mm) and hydro-electric potential for the low, mid and high elevation belts in the Ursern valley (for the belt as a whole and per ha) as determined in this study and in the Inauen *et al.*, study (2013).

Belt	Study	Runoff	Hydro-electric potential	
(falling height)		mm	kCHF (kEUR)	CHF (EUR) ha^{-1}
L (1600)	This study	18 – 54	94 – 281 (86 – 259)	33 – 99 (30 – 91)
	Inauen	30 – 74	156 – 385 (144 – 355)	55 – 135 (50 – 124)
M (2000)	This study	0 – 0	0 – 0 (0 – 0)	0 – 0 (0 – 0)
	Inauen	30 – 74	558 – 1377 (514 –1267)	95 –234 (87 –215)
H (2400)	This study	0 – 0	0 – 0 (0 – 0)	0 – 0 (0 – 0)
	Inauen	22 – 35	728 – 1159 (670 – 1066)	78 – 123 (71 – 114)

Discussion and conclusions

We investigated immediate (cut versus uncut) and long-term (dwarf shrub presence) effects of abandonment on the water balance in grassland ecosystems along an elevational gradient. Besides the natural decline of ET with elevation due to reduced atmospheric forcing and biomass (Van den Bergh *et al.*, 2013), we found that land abandonment (long grass) causes an increase in bright day ET (WLET). Abandonment effects were positively associated with plant biomass (LAI) and were larger at montane (L and M) than at alpine elevations (H). The abandonment was most pronounced early in the growing season and diminished with time, because of reduced day length and plant senescence.

The range of land cover types employed ranged from low stature herbaceous vegetation with ET rates and biomass as low or similar as in clipped swards. Dwarf shrubs (L and M) and tall *Agrostis* and *Deschampsia* swards (H) resemble the maximum height after long term abandonment. Dwarf shrub encroachment has been shown to alter canopy structure and composition and has been associated with reduced albedo and increased ET (Myers-Smith *et. al.*, 2011). Still, our data show that *Calluna* and *Vaccinium* exhibit ET rates intermediate between clipped and abandoned grass swards. Therefore, colonization by dwarf shrubs is expected to reduce initial abandonment related increases in ET. Yet, dwarf shrubs lose more water than a grazed (cut) turf, probably because of greater leaf area and better aerodynamic coupling of foliage than in short grass swards. Konzelman and co-workers (1997) compared ET rates from a mown grassland to those from dwarf shrub vegetation (*Rhododendro-Vaccinietum*) and found lower ET rates in dwarf shrubs. In contrast, our Vaccinium dominated communities had ET rates higher than in clipped swards. At the high site, *Agrostis* and *Deschampsia* ET showed much stronger abandonment responses than the three most common grassland types at high elevation. Hence, it seems likely that, in contrast to montane sites, for alpine elevations, increases in ET become more pronounced over time as taller grasses become more abundant.

Compared to WLs, clipping effects on ET in DSCET were smaller, because of the inclusion of overcast and rainy days not included in WL data. For this reason also, warm and dry summers produced stronger land use signals than slightly cooler and more humid summers as were covered by Inauen *et al.*, (2013). All-weather ET measurements by DSCs are considerably more difficult to interpret than bright day measurements because a number of additional processes come into play. For instance, dew formation can be substantial in alpine vegetation (de Jong *et al.,* 2005) and tall swards are likely to capture more dew. Interception losses of precipitation, on the other hand, can be expected to be largest for abandoned grassland and may compensate for higher dew interception.

Obojes *et al.* (2014) compared grassland DSCET across the Alps (France, Switzerland and Austria), during the 2008 growing season. They found that ET increases with biomass at all sites but that effect of species composition was site specific. Herb abundance was positively related to DSCET at the Austrian site which was explained by the high leaf conductances that are typically observed in herbaceous vegetation (Körner and Mayr, 1981, Körner 2003). In our study, high ET rates were observed in grass and herb dominated swards while in *Nardus*, ET was commonly lower. Overall however, species composition was less important than elevation and biomass (clipping treatment).

Our study simulated sustainable biomass removal by grazing (or grazing and mowing at low elevation), and thus, did not account for severe disturbance effects of overgrazing (trampling, erosion). Trampling may lead to soil compaction and increases bare soil surface; (e.g. Tate *et al.,* 2004). Trampling can however, increase ET as was shown by Scott *et al.* (2002) by increasing soil evaporation. Intense trampling has also been shown to reduce infiltration and enhance runoff (Leitinger *et al.*, 2010).

In line with our data, a hydrological model has demonstrated substantial reductions in catchment runoff due to abandonment (Fatichi *et al.*, 2014). Inauen and co-workers

(2013), in an attempt to quantify the economic costs associated with grazing cessation, arrived at substantially higher effects on DSCET This discrepancy is likely the result of differences in weather conditions between years and the different grassland types considered. At the low site we have demonstrated that abandonment leads to higher DSCET regardless of weather conditions. In contrast, at high montane and alpine elevations such effects may be substantial for growing periods with good weather conditions but they may also approach zero under less favourable conditions. For high montane sites, effects are potentially most substantial as for alpine conditions, smaller abandonment effects are only partly compensated for by a greater falling height.

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Chapter 4

Alnus shrub expansion increases evapotranspiration in the Swiss Alps

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Abstract

Shrub encroachment is one of the main consequences of abandonment of montane grassland. Higher surface roughness of shrubs leads to stronger aerodynamic coupling. This should increase evapotranspiration (ET), but lower surface temperatures (due to higher ET and reduced aerodynamic resistance) could again counter this effect. We explored this question by employing weighable lysimeters in adjacent grass- and shrubland understorey, and by measuring canopy transpiration in *Alnus* with sap flow sensors at 1675 m a.s.l. in the Swiss central Alps. For 11 bright days, ET rates of *Alnus* clearly exceeded those from grassland by on average 31 ± 14 % or 1.2 ± 0.6 mm d^{-1} (mean ± sd). During days with high VPD, differences in ET were largest, indicating that enhanced aerodynamic coupling had a greater influence than evaporative cooling. Cooler Alnus than grassland canopies were confirmed by infrared thermography. For the growing season (mid May – end of September), we estimate that this increase in ET results in a reduction in runoff by 78 to 81 mm (2010, 2011). Accounting for the falling height of water, this lower runoff reduces the hydro-electric potential of the upper Reuss catchment (227 km^2) by 0.47 Mio CHF per growing season (same amount in US$; *Alnus* cover analysed for the year 2004/05) and by 1.8 Mio CHF for a scenario where all grasslands below the natural treeline would be converted into shrubland. So, shrub encroachment exerts clear hydrological drawbacks.

Keywords

Alder, hydrology, land use, mountains, sap flow, transpiration

Introduction

Shrub encroachment occurs across all continents (van Aucken, 2000; Roques *et al.,* 2001; Maestre *et al.,* 2009). The reasons for it vary but are often related to global change, particularly, to altered land use. In tropical regions, reduced grazing and lower fire frequencies have allowed shrubs and trees to colonise grasslands and savannas (Fairhead and Leach, 1996; Scholes and Archer 1997; Roques *et al.,* 2001). In temperate and boreal areas, shrub encroachment has often been associated with land abandonment and climatic warming (Sturm *et al.,* 2001; Tape *et al.,* 2006; Morgan *et al.,* 2007; Navarro and Pereira, 2012).

In the Swiss Alps, land abandonment has led to large-scale shrub encroachment (MacDonald *et al.,* 2000; Tasser *et al.,* 2005; Gellrich *et al.,* 2007). Between 1912 and 1997, 34% of all montane and alpine pastures have been abandoned (Baur *et al.,* 2007) which has led to a doubling of shrub and forest cover (Huber and Frehner 2013). The tall (2 m), N_2-fixing *Alnus viridis* ([Chaix] D.C.; green alder) is a dominant species in these newly established shrublands and forms extremely dense thickets. After *Alnus* has taken over, further succession towards conifer forest is extremely slow due to the high rates of nitrogen fixation of *Alnus* and the resulting dense canopies, jointly preventing the establishment of trees (Tappeiner and Cernusca, 1993; Gehrig-Fasel *et al.,* 2007; Hiltbrunner *et al.,* 2014).

Shrub encroachment strongly affects ecosystem structure and functioning (Eldridge *et al.,* 2011, 2012). Surface roughness and above-ground biomass production increase (Knapp *et al.,* 2008) but albedo is reduced (Chapin *et al.,* 2005). Increased leaf area per ground area (LAI) and the spatial arrangement of the shrub's foliage affect canopy transpiration but also rainfall interception and throughfall (Brechtel, 1996). Often, soil C and N stores increase in expanding shrubland (Montané *et al.,* 2007; Brantley and Young, 2010) but consequences depend also on species composition (Eldridge *et al.,* 2011). Expansion of *Alnus* results in significant nitrogen (N) enrichment and higher N

losses through nitrate leaching and gaseous N emissions (Bühlmann *et al.,* 2014; 2016; Hiltbrunner *et al.,* 2014). Impacts on the catchment water balance are less well known, and will be explored here.

Effects of afforestation and deforestation on catchment water yield have already been studied for decades (Bosch and Hewlett, 1982). Generally, afforestation leads to higher landscape water use, mainly through increased evapotranspiration (ET), while deforestation increases catchment discharge (Lorup *et al.,* 1998; Brown *et al.,* 2005; Farley *et al.,* 2005). For alpine grassland it has been shown that abandonment and the associated increase in plant height and leaf area, raises ET by about 10% (Körner and Nakhutsrishvili, 1986; Körner *et al.,* 1989; Tappeiner and Cernusca, 1998; Inauen *et al.,* 2013). Because of a more pronounced increase in biomass following abandonment, hydrological effects are much larger and ET can increase by up to 40% for bright days in montane grassland (Obojes *et al.,* 2014; Van den Bergh 2017). However, the falling height of water is less from montane compared to alpine elevations, and in the central Alps, the land area is also larger in the alpine belt, hence, effects on the hydro-electric potential of a catchment are commonly larger at alpine elevations,.

Shrubland and forest typically exhibit low surface runoff coefficients (e.g., Bunza, 1978; Markart *et al.,* 2006; Schleppi 2010). Under simulated, extreme rain events (30 mm in 15 minutes), runoff reached 40% of precipitation for grazed montane grassland, while in green alder, runoff amounted to 16% only (Tappeiner and Cernusca, 1993). *Alnus* expansion has thus been associated with increasing soil hydraulic conductivity and porosity (Alaoui *et al.,* 2014) but soil stability tends to decrease (Tasser *et al.,* 2003; Caviezel *et al.,* 2014). These findings do however, not indicate whether and how the seasonal water balance is affected by the transition from grass- to shrubland. Given the large spatial extent of newly established shrubland, this is of considerable interest for water supply to the tele-connected lowlands and for hydro-electric power generation in mountain catchments (Viviroli and Weingartner, 2004; Rahman *et al.,* 2015).

From theory it is not *a priori* clear whether taller shrub canopies use more or less water than the grassland they replace. Shrubs are aerodynamically better coupled to atmospheric circulation which facilitates vapour transfer. Canopy temperatures are likely to be lower (either due to higher ET or better aerodynamic coupling), which should reduce leaf to air vapour pressure gradients and hence, leaf transpiration (Larcher, 2012; Jones, 2014). *Alnus* is known to keep its stomata open even under high vapour pressure deficits (VPD; Körner *et al.,* 1978; Herbst *et al.,* 1999). Here, we aim at quantifying the net effect of such influences on evapotranspiration after *Alnus* establishment into montane grasslands. Overall, we expect land abandonment and *Alnus* establishment to lead to higher ET. Because higher ET means reduced runoff, we also expect that the catchment hydro-electric potential to be reduced as a consequence.

Material and methods

Classically, ET is obtained at catchment scale by solving the water balance equation from rainfall and river discharge measurements. Particularly for mountain valleys with large proportions of the land far above the treeline, this approach does not work. Rainfall can vary enormously with data from a single station coming close to a lottery with regard to the entire catchment input (Wood *et al.,* 2000; see also de Jong *et al.,* 2002). Residence times of water in aquifers are unknown, water shed delineation and water diverted to other catchments all add significant errors. Further, river discharge during the growing season is dominated by snow- and glacier-melt, which vary from year to year and over time with climatic warming. Finally, for the valley where we set up our measurements, the land area occupied by *Alnus* is only 7%, causing the above uncertainties and errors to mask such a land use signal. Therefore, we aimed at quantifying the differences in ET from grassland and green alder directly, employing weighing lysimeters and measurements of water flow in *Alnus* stems (xylem sap flow).

Study site

To assess the effects of shrub encroachment on ecosystem water use, we set up an experiment where we simultaneously measured ET rates of grassland and green alder shrubs at a north exposed site where both vegetation types co-occur in the west-east oriented Ursern valley in the Swiss central Alps. The still open grassland was grazed by cattle. The *Alnus* stand at the site was mature and several decades old. The site is north exposed, located at 1675 m a.s.l. (46°36'49'' N, 8°34'2'' E) with an acidic, sandy loam soil. The grassland was dominated by *Nardus stricta* and had a canopy height of 5 to 15 cm. Shrub height ranged between 1.5 to 2.0 m. *Alnus viridis* [Chaix] D.C. was the main canopy constituent (70 to 80% of the overstorey leaf area) with some scattered *Sorbus aucuparia* L. individuals. The understorey cover was composed of dwarf shrubs [*Vaccinium myrtillus* (L.), *Vaccinium vitis-idaea* (L.), grasses (*Milium effusum* (L.)] and tall herbs that are typically found in places with high nitrogen availability (*Adenostyles alliariae* (Gouan) [A. Kern], *Cicerbita alpina* L. [Wallr.], etc.). The distance between the studied *Alnus* stand and the grassland was *c*. 30 m.

Weather data

The climate of the region is humid with precipitation normally exceeding evapotranspiration during the *ca*. 5-month growing season (May – September). Annual precipitation averages 1485 mm with approximately half of that amount falling during the growing season. The warmest month mean air temperature is 13.1 °C (July, weather station Andermatt, run by the Federal Office of Meteorology and Climatology MeteoSwiss, 2015). A weather station was installed at the grassland site (Davis Vantage Pro2, Davis Instruments Corp. Hayward, CA, USA) measuring air temperature, relative humidity, wind speed and solar radiation.

Canopy temperature

We measured surface temperatures of grassland and *Alnus* shrubland for a bright day using an infrared camera (VarioCam HR, InfraTec GmbH, Dresden, Germany; sensitivity: 7.5–14 µm of the electromagnetic spectrum, resolution: 320 × 240 pixels). A thermal image was taken from the opposite side of the valley viewing the same slope as for the ET study but for accessibility reasons, at a more westward position (elevation *ca.*1850 m a.s.l at *c.* 800 m viewing distance). We processed the thermal image (taken on the 23rd of September 2009 at 2:40 pm) using IRBIS software (InfraTec, Jena, Germany). We used a constant emissivity of e = 1 (Scherrer and Körner 2009 GCB) and averaged the surface temperature readings of four rectangular areas in pastures (around 1650 m a.s.l.) and four areas in *Alnus* shrubland (around 1750 m a.s.l.; 15x15m plots of similar exposure). Reference air temperatures were available from two nearby weather stations at 1495 and 1950 m a.s.l. (Davis Vantage Pro2, Davis Instruments Corp. Hayward, CA, USA). The lower weather station was located on a south-exposed grassland slope whereas the one at the higher site was on more level terrain (for details see Van den Bergh *et al.,* 2013).

Grassland evapotranspiration

We measured grassland ET by means of 16, 20-Liter monolithic, weighable lysimeters (WL) which were weighed before local sunrise and after local sunset on an electrical balance in an on-site shelter (installation in spring 2010; previous experiments have shown that night time ET is generally negligible (Van den Bergh *et al.,* 2013). Grassland monoliths were selected at the study site and were typically dominated by *Nardus stricta, Deschampsia caespitosa, Festuca* sp. and a wide range of herbaceous species such as *Alchemilla* sp., *Arnica montana* (L.), *Euphrasia* sp., *Geum montanum* (L.) *Parnassia palustris* (L.), and *Potentilla erecta*. Daytime grassland ET was determined for a total of 23 bright days during the growing seasons of 2010 and 2011. Weather conditions during these days corresponded to what is common at this elevation for rainless summer days (we use the term bright for such days with commonly clear mornings and typical afternoon clouds).

Alnus bush evapotranspiration

We measured sap flow rates of *Alnus* stems scaled to stand level and added understorey ET to arrive at ecosystem ET rates. *Alnus* understorey ET was measured by seven weighable lysimeters (same as in grassland, same days), filled with understorey monoliths in 2011 (five days). After ET measurements, above-ground phytomass was harvested of all WLs (phytomass was sorted into biomass, necromass and cryptogam mass).

The rate of transpiration in Alnus was calculated from sap flow data obtained from stems using the energy balance method (SGB-19WS sensors, named Dynagage sensors hereafter, attached to the Dynagage Flow32-1K sap flow system, Dynamax, Inc. Houston, TX, USA.). Following manufacturer instructions (Dynamax Inc., 2005), we mounted sensors to 16 representative stems during the growing season of 2010 and 2011 (two sensors failed, so we ended up with data from 14 sensors). We collected one series of data in 2010 (running from Aug 13 until Sept 13; ten sensors fitted on *Alnus* and four

on *Sorbus*) and two series in 2011 (June 15- until July 4 and July 7 until Aug 25; for both runs, 11 sensors were installed on *Alnus* and three on *Sorbus*). Average sensor signals were recorded at 10 min intervals on a CR1000 data logger (Campbell Scientific, Logan, UT, USA). Assuming steady-state conditions (i.e., no change in heat storage), stem sap flow can be calculated as the residual of the energy balance (Sakuratani, 1981; Sakuratani, 1984; Baker and Van Bavel, 1987). To obtain daily stem transpiration, sap flow readings were summed up for the same time period during which we performed our grassland and understorey ET measurements with weighing lysimeters. For the season 2010, grassland ET and stem sap flows were measured simultaneously during six days and in 2011 during five days. From correlations between grass and shrubland ET rates and weather data, we established two simple linear regression models to estimate daytime grass and shrubland ET for the growing seasons of 2010 and 2011 (mid May – end of September).

To test the accuracy of the sap flow sensors, we compared the transpiration rates estimated by the Dynagage sensors with the concurrent 'true' water consumption of cut stems taking water from a reservoir ('potometers') during two days at the end of the second series of sap flow measurements in 2011. Stems were cut twice with a pair of bypass loppers (second cut was underwater) and put in 1L graduated cylinders filled with pre-boiled water. Water loss by transpiration was determined by refilling cylinders every 1 or 2 hours to a fixed level using a graduated pipet.

Up-scaling stem sap flow rates to stand level

To arrive at canopy ET rates, we scaled sap flow rates from single stems to the entire shrub canopy using the leaf area – sap flow relationships of all stems equipped with Dynagage sensors. Leaf area per stem was determined from a representative subsample by a leaf area meter (LI 3100, LI-COR, Lincoln, NE, USA). Leaf samples were dried at 80 °C for 96 hours and then weighed to calculate specific leaf area (SLA, $kg\ m^{-2}$).

The next step was to quantify canopy leaf area for *Alnus* stands. Along two 20 m long and 2 m wide transects we recorded mean stem diameter (20 cm above ground level) for all stems. We sampled a total of 426 *Alnus* and 105 *Sorbus* stems (mean stem diameter of 22 ± 15 and 20 ± 16 mm, respectively [mean ± sd]). For damaged stems, we estimated the fraction of remaining leaves as compared to a vital stem of the same diameter (some stems were infested by a wilting disease that is common in *Alnus*). A generic, allometric model was then developed to relate leaf area (obtained from leaf dry weight by SLA) to stem diameter for 33 healthy *Alnus* and 32 *Sorbus* stems differing in stem diameter (*Alnus*: 4 - 92 mm; *Sorbus*: 7 - 105 mm). The allometric model and the stem diameter census was then used to calculate stand leaf area per unit ground area. Finally, we compared these allometry based leaf area indices (LAI) with *in situ* LAI estimates obtained from light interception measurements (ceptometer, AccuPAR LP-80, Decagon Devices Inc., Pullman, WA, USA). Ceptometer LAI readings were corrected by leafless stem area index (measured after leaf fall). Shrubland ET was then calculated by scaling sap flow rates of single stems to the full canopy. Finally, we added understorey ET. For the days with missing understorey ET data, these were estimated as a fixed fraction of the shrub canopy transpiration (mean of the available five days).

Alnus leaf conductance measurements

As an indication of on-going stomatal control of transpiration under high evaporative forcing, we measured leaf diffusive conductance of *Alnus* foliage with a porometer (SC-1 leaf porometer Decagon Devices Inc., Pullman, WA, USA) in a south-east sloping *Alnus* stand (46°35'30'' N, 8°29'07'' E, *c.* 1900 m a.s.l.) during two sunny days in August in 2012 (Aug 7 and 8). Leaf conductance readings were obtained from four solitarily standing shrubs and from four shrubs within a dense stand. For each shrub, we measured repeatedly leaf conductance of three sun and three shade leaves to obtain daily courses in leaf conductance. During these porometer measurements air

temperature and humidity were measured manually using a sling psychrometer (Bacharach, Inc., New Kensington, USA).

Effects on growing season ET and catchment hydro-electric potential

From correlations between weather parameters and ET of grassland and *Alnus*, we developed two simple regression models to estimate ET rates for the days where measured ET data was unavailable. From these daily ET sums for both vegetation types we calculated differences in ET across the entire growing season (mid May – end of September).

Land cover assessment

The current land area covered by *Alnus* shrub in the Ursern valley was estimated by manually delineating shrub cover in ArcGIS using SWISSIMAGE ortho-photos (2004/05) as a reference. These polygons were transformed into a grid with a resolution of 2 x 2 meters. The size of the Ursern valley catchment was defined using the 'watershed' tool from ArcGIS and the swissALTI3D digital elevation model (Swisstopo; resolution: 2 x 2 m; for the details see Van den Bergh 2017, in press).

Effects of the *Alnus* expansion on the catchment's hydro-electric potential were calculated for seven 100-m-elevational belts, from valley bottom at 1440 m to 2100 m a.s.l. (current potential climatic treeline). We used the mean elevation of each of these belts as the falling height (1450 m, 1550 m, etc.), the mean difference in ET between grassland and *Alnus* (for the growing seasons of 2010 and 2011), a producers price for electric energy of 0.09 CHF kWh^{-1} (in Switzerland electricity prices are more or less equally made up of grid maintenance, taxes and electricity costs: Eidgenössische Elektrizitätskommission ElCom 2013) and an efficiency of 85% of hydro-electric power plants in order to arrive at estimates of the 'electricity'-costs of the *Alnus* shub encroachment in the upper Reuss catchment in the year 2004/05. In addition, we

scaled the differences in ET to a situation in which all potential *Alnus* habitats in the selected area were invaded by *Alnus* (corresponding to 67 km^2).

Statistical analyses

Calculations and analyses were performed using the open-source software R, version 2.15.2 (R Development Core Team, 2010). For testing whether differences in ET rates between grassland and shrubland were significant, we used linear mixed effect models implemented in the *nlme* package (Pinheiro *et al.,* 2011). Grassland lysimeter and Dynagage sensor were treated as random effects. We determined the optimal variance structure using likelihood ratio tests (fitted with restricted maximum likelihood). The minimal adequate model was determined by comparing a reduced model (removing non-significant variables) to the full model. We used Tukey's HSD tests for comparing group means from the *multcomp* package of R (Hothorn *et al.,* 2008). For these mixed effect models, normality and homogeneity of variances of the residuals were assessed visually. Log or power transformations were applied where necessary. Differences between means were considered statistically significant at $p<0.05$ (* signs in figures indicate significance of differences *: $0.05 \geq p \leq 0.01$; **: $0.01 \geq p \leq 0.001$;***: $p \leq 0.001$).

Results

Climatic data

Shrub canopies are indeed cooler than grassland under bright weather conditions. Infra-red thermal images revealed that *Alnus* shrub surface temperatures were on average 4.4 K lower than those of adjacent grassland (Fig. 1). The small difference in elevation (1740 to 1920 m a.s.l.) did not significantly affect the mean shrub surface temperature of 14.6 °C which was similar to the concurrent air temperatures of 16.9 °C and 14.4 °C measured at the two nearby weather stations at 1490 and 1960 m a.s.l. Shrubs are aerodynamically better coupled to atmospheric circulation which facilitates vapour transfer. Canopy temperatures are likely to be lower (either due to higher ET or better aerodynamic coupling), which should reduce leaf to air vapour pressure gradients and hence, leaf transpiration (Larcher, 2012; Jones, 2014).

Mean daytime air temperatures during the ET measurements were slightly higher in 2010 than in 2011 (Table 1). Mean vapour pressure deficit (VPD) and wind speed were similar for those days in both years, while solar radiation was slightly higher in 2011.

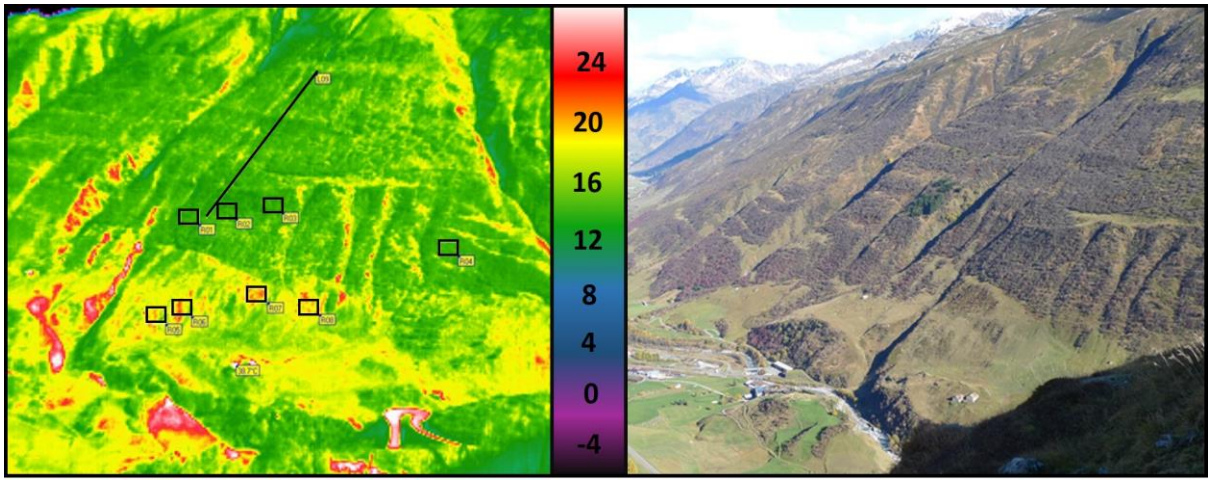

Fig. 1 Infra-red thermogram (left) showing surface temperatures of a north exposed grassland – *Alnus* slope between 1700 and 1900 m a.s.l. Boxes indicate the test areas that were used for calculating average grass and shrubland surface temperatures. The line indicates the transect between from *c.* 1740 m to 1920 m a.s.l. Thermogram was taken on the 23rd of September in 2009 at 2:40 pm. Digital photo (right) was taken the 24th of October in 2012 (*Alnus* has shed its foliage by this date).

Table 1. Daytime weather conditions (mean ± sd) during ET measuring days (simultaneously in grassland and *Alnus*) of 2010 and 2011 (number of days). Daytime corresponds to the time period between local sunrise to local sunset.

Year	Air temperature (°C)	VPD (kPa)	Wind speed ($m\ s^{-1}$)	Solar radiation ($MJ\ d^{-1}$)
2010 (6)	14.8 ± 3.4	0.61 ± 0.32	1.7 ± 0.5	19.0 ± 3.3
2011 (5)	13.6 ± 2.8	0.58 ± 0.24	1.8 ± 0.5	21.5 ± 4.9

Evapotranspiration

The allometric data for scaling from stem diameter to leaf dry matter in *Alnus* and *Sorbus* yielded similar exponential relationships for both species and became linear after log-log transformation (Fig. 2). Including *'species'* and *'species* x *stem diameter'* did not improve the model fit. Thus, leaf mass was calculated from stem diameter as follows (R^2=0.96, $F_{(1, 63)}$=1366, p<0.001):

$$\text{Leaf mass} = \text{stem diameter}^{2.19} \times 10^{-1.38} \qquad \text{Eq. 1}$$

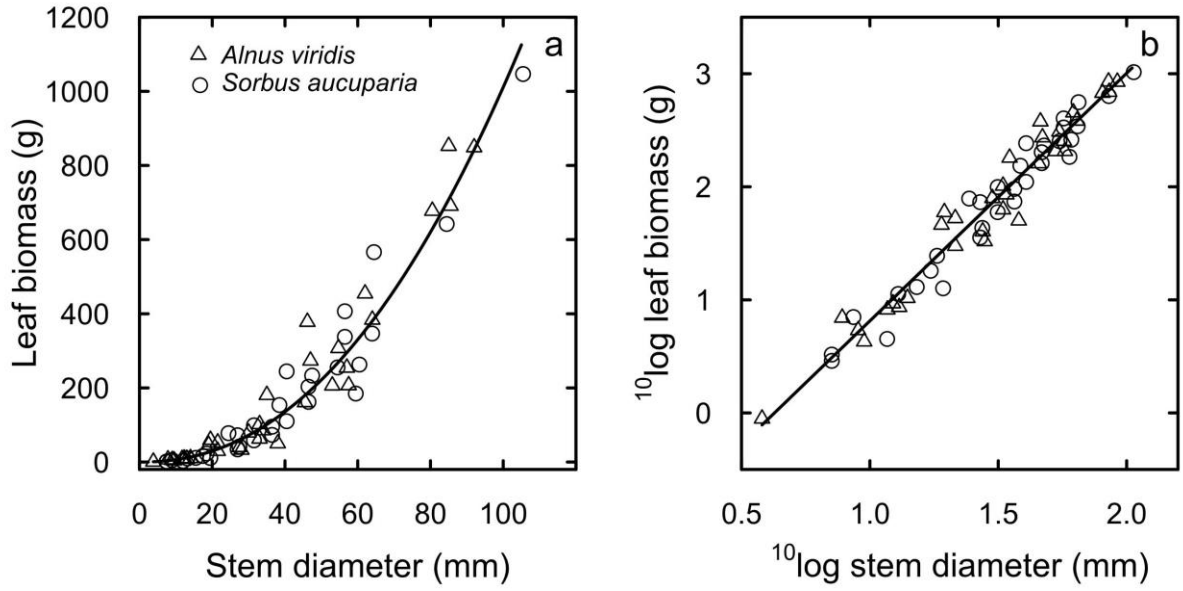

Fig. 2 Leaf biomass as a function of stem diameter for *Alnus viridis* (n=33 stems) and *Sorbus aucuparia* (n=32 stems; a) non- transformed data for leaf mass and stem diameter, b), log-log plot)

For the entire shrub canopy we arrived at a leaf mass of 287 ± 33 g m^{-2} and an LAI of 3.4 ± 0.4 m^2 m^{-2} (mean ± sd). *Alnus* made up 79% of the overstorey leaf area. *Sorbus* accounted for the remaining 21%. Light interception measurements in a nearby *Alnus* stand as well as along the transects confirmed these estimates and yielded similar LAI values of 3.7 ± 0.1 m^2 m^{-2} (mean ± sd).

For the grassland monoliths, aboveground biomass was 359 ± 135 g m^{-2} (mean ± sd), with similar amounts of necromass (331 ± 224 g m^{-2}). Cryptogams (lichens, mosses) contributed little to monolith phytomass (6 ± 8 g m^{-2}). In understorey lysimeters (year 2011), leaf biomass was 376 ± 216 g m^{-2} , thus slightly higher than in the grassland but necromass and mosses were absent.

Sap flow rates obtained with the heat balance method agreed well with 'true' stem water use during the first day of the potometer experiment (Fig. 3; the slope of the regression was not significantly different from the 1:1-line: β=-0.12 ± 0.07, $t_{(33)}$=-1.8, p=0.08 and the intercept was not significantly different from zero $t_{(33)}$=0.3, p=0.75; Fig. 3). During the second day, the Dynagage sensors showed slightly higher transpiration rates than potometers (β=-0.35 ± 0.04, $t_{(63)}$=-8.9, p<0.001; $t_{(63)}$=2.3, p=0.03) possibly due to temporary violations of the steady state energy balance assumption (Grime and Sinclair, 1999; Baker and Van Bavel, 1987). In the long run, however, such deviations should cancel each other, hence, we applied no corrections to the calculated sap flow rates.

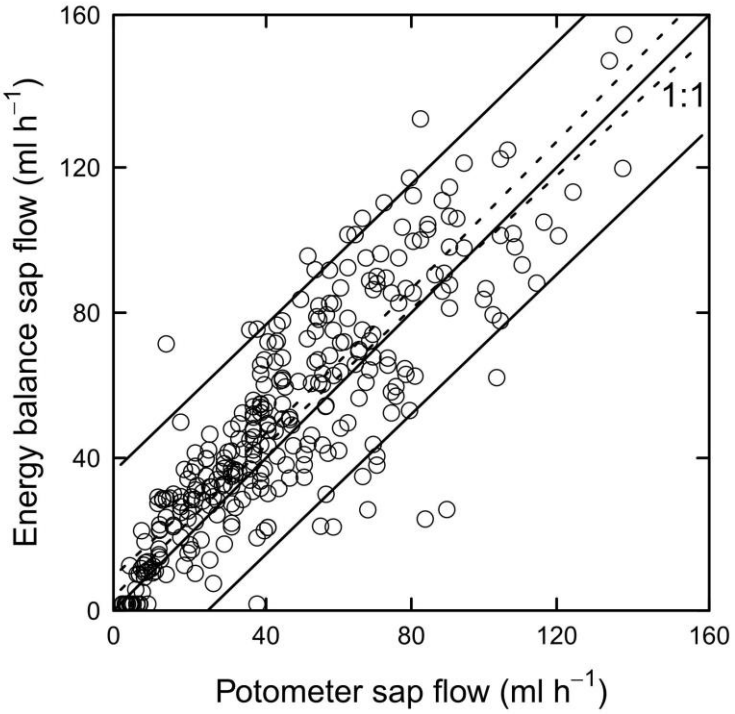

Fig. 3 Comparison of sap flow rates measured by the energy balance method (dynagage sensors) and by potometers in 14 cut stems (first day of potometer experiment only; n= 11 *Alnus* and n=3 *Sorbus).* Dashed line indicates 95% confidence interval of the regression, dotted lines show the predicted 95% CI

Alnus and *Sorbus* stems showed similar daily transpiration rates per unit of leaf area (*'species'* did not significantly improve the statistical model in two out of three sap flow runs: series 1, 2010: $F_{(1, 414)}$=1.06, p=0.303; series 1, 2011: $F_{(1, 278)}$=4.97, p=0.027; series 2, 2011: $F_{(1, 628)}$=0.03, p=0.870). The significant (though small) species effect for the first series of sap flow measurements in 2011 possibly resulted from differences in phenology between *Alnus* and *Sorbus* (different leaf-out time). Hence, stem sap flow rates were scaled to the full canopy without considering the relative abundance of both species.

Across the five sampling days in 2011, mean understorey evapotranspiration reached 37% ± 10%, (mean ± sd) of the overstorey sap-flow-derived ET. It decreased with time, most likely because of plant senescence, particularly in the tall herbs. For days with

missing understorey ET, we multiplied overstorey ET by 0.37 to estimate the understorey contribution (all 2010 sampling days). The combined understorey and overstorey ET for 2010 (5.0 ± 0.9 mm d^{-1}) significantly exceeded concurrent grassland ET (3.7 ± 0.6 mm d^{-1}) by 33 ± 15% ($F_{(1, 158)}$=10.1, p=0.002; *Fig. 4*). Similarly, in 2011 shrubland ET (5.1 ± 1.1mm d^{-1} for 11 days) exceeded grassland ET by 26 ± 13% (4.1 ± 0.8 mm d^{-1}; $F_{(1, 145)}$=12.8, p<0.001). On ten of the eleven sampling days, ET differences between grass- and shrubland were statistically significant. On average, the difference in ET between grass- and shrubland was 1.2 ± 0.6 mm d^{-1}.

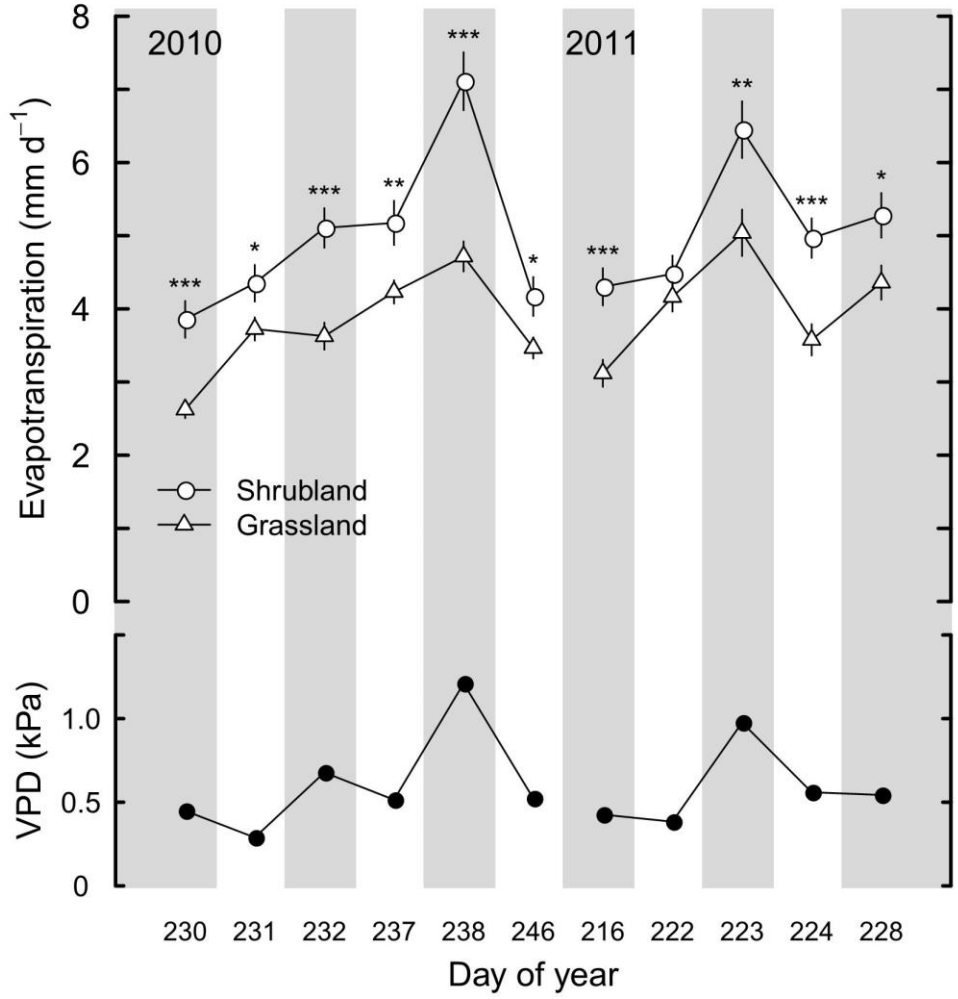

Fig. 4 ET rates (mean ± se) of grass- (different grassland types combined) and of shrubland and mean daytime VPDs during 6 and 5 sampling days in 2010 and 2011 (points are connected for clarity only).

Using the on-site weather data, grassland ET most strongly correlated with VPD (β =1.83, $t_{(20)}$=7.6, p<0.001) and solar radiation (β =0.16, $t_{(20)}$=10.7, p<0.001) but not with wind speed (overall R^2_{adj}=0.93, p<0.001, n=23 days). Shrubland ET was best explained by VPD (β =2.53, $t_{(93)}$=8.9, p<0.001), wind speed (β =-0.36, $t_{(93)}$=-1.9, p=0.05) and solar radiation (β =0.10, $t_{(93)}$=6.3, p<0.001; overall R^2_{adj}=0.79, p<0.001, n=96 days). These linear regression models were then employed to estimate daytime grass- and shrubland ET for longer periods and the growing seasons 2010, 2011 (from mid May until end of September).

The negative effect of wind on the shrubland ET resulted most likely from confounding by other factors. For the days covered in the sampling period (not only the 11 bright days), sap flow appeared to saturate at VPD levels of 1.5 kPa (Fig. 5). However, conditions with such high evaporative demand were rare in the study region. Our porometer measurements on *Alnus* leaves showed a high leaf conductance of around 400 mmol m^{-2} s^{-1} under full sunlight, and no mid-day depression in transpiration due to closure of stomata (Fig. 6). Stomatal conductance was generally higher in sun compared to shade leaves (sun, shade leaves nested within individual: $F_{(2, 138)}$=52.9, p<0.001) and leaves of solitarily standing bushes exhibited slightly higher conductance compared to leaves in a dense stand ($F_{(2, 138)}$=11.7, p<0.001).

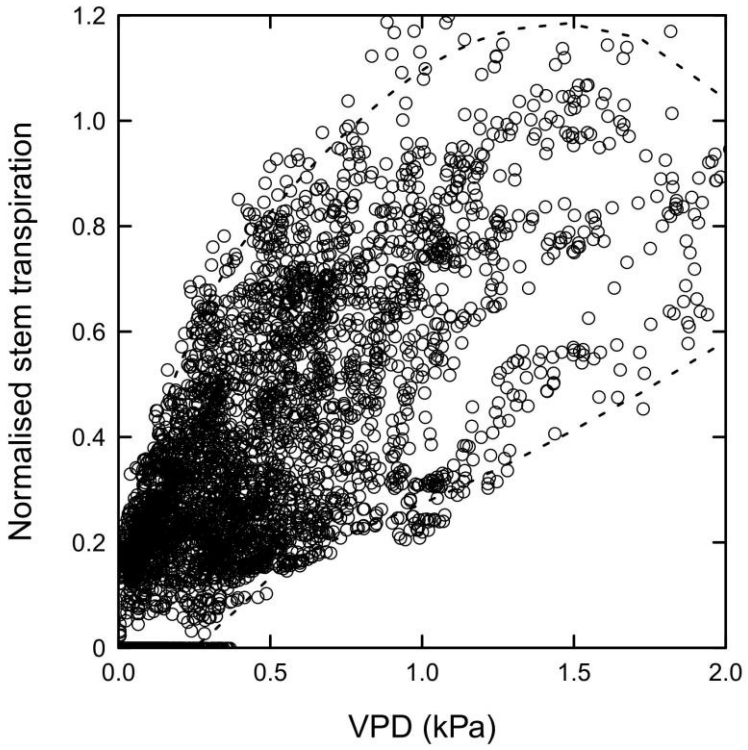

Fig. 5 Normalised 10-min dynagage sap flow rates (normalised to the 99 percentile) in relation to VPD (sap flow measurements in 2011, July 7 until August 25). Dashed lines show smoothed boundaries at 0.025 to 0.975% quantiles.

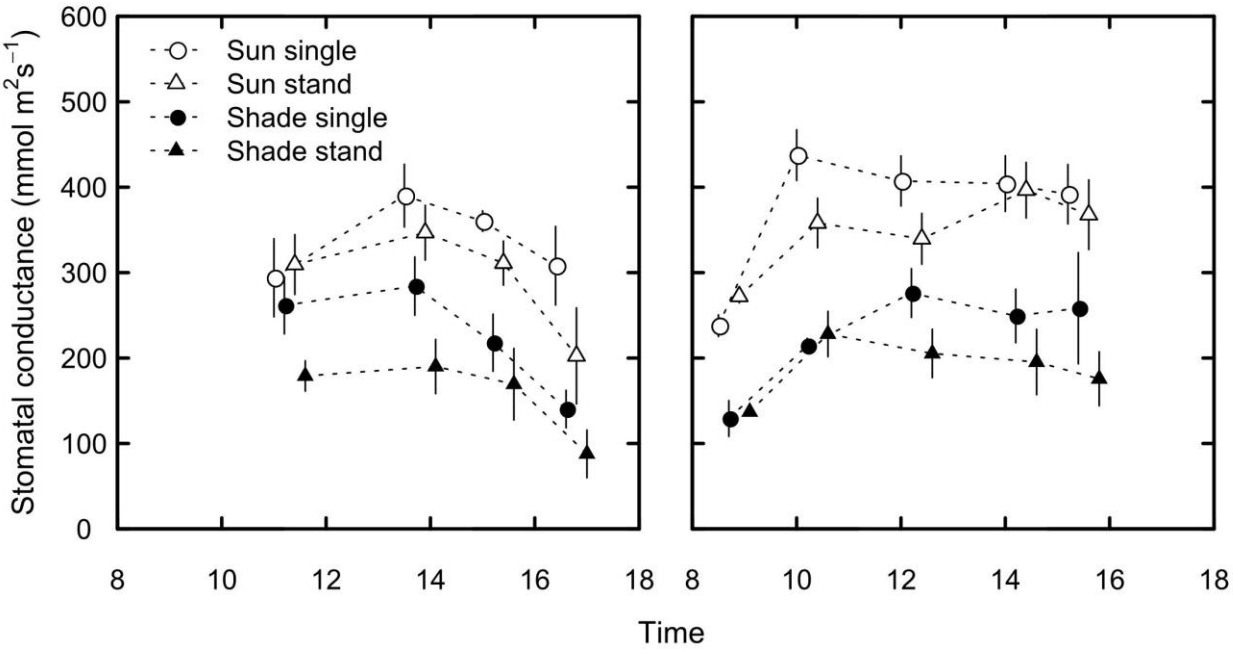

Fig. 6 Diurnal courses of stomatal conductance (mean ± se) in *Alnus viridis* leaves. Sun and shade leaves of solitarily standing *Alnus* bushes and of *Alnus* in a dense stands were measured during two sunny days in 2012 (August 7, 8)

Using the two regression models for the period of 96 days during which sap flow measurements were performed, shrubland ET exceeded the estimated grassland ET by 55 mm or 18%. And also for the full length of the growing seasons 2010 and 2011, shrubland ET was 78 and 81 mm higher than the grassland ET (20 and 21%, respectively).

Land cover assessment

The upper Reuss catchment including the Ursern valley spans elevations from 1440 to 3590 m a.s.l. and covers almost 227 km². Below 2100 m a.s.l., thus in the montane forest zone, grassland covered 49 km² (values valid for the year of the ortho-photos, i.e., 2004/05). *S*hrubland covered 16 km². The other land cover types (forest, settlements, lakes and waters, bare lands, scree and rocks) made up 8 km². Above 2100 m a.s.l. grassland extended over an area of 94 km² and other land cover types amounted to 65 km². We estimate that for 16 km², *Alnus* shrublands reduce the potential hydro-electric power yields by 0.46 to 0.48 Mio CHF per growing season compared to the former grassland state. A complete transition of all remaining grassland below 2100 m a.s.l. into shrubland (49 km²), would further reduce the hydro-electric potential of the valley by around 1.35 to 1.40 Mio CHF per season, hence the total financial losses due to the conversion of all grasslands into shrubland would arrive at 1.81 – 1.88 Mio CHF per growing season.

Discussion and conclusions

We have shown that the current widespread colonisation of montane pastures and meadows by green alder increases ecosystem ET rates, inevitably reducing runoff during the growing season. Differences in ET were particularly pronounced during days with strong atmospheric forcing (high VPD), indicating that enhanced aerodynamic coupling is an important factor explaining these higher ET rates. Thus, both, stronger coupling to ambient air conditions and higher ET contributed to the lower foliage temperature in *Alnus* shrubland compared to grassland as evidenced by thermal imaging. This higher ET diminishes the hydro-electric potential of the catcment.

Heinl *et al.,* (2012) monitored the surface temperatures of different land cover types by IR images in the Austrian Alps. Similar to our observations, surface temperatures in montane grassland (both, grazed and abandoned) were clearly higher than air temperature, whereas in conifer forests, surface temperature closely followed air temperature (Körner 2007). With its broader leaves and shorter stature, *Alnus* is less well coupled to the free atmosphere than conifers (as was found for mixed broad-leaved - conifer forests; Leuzinger and Körner 2007), but higher evaporative cooling appears to compensate for that.

The sap flow rates used to calculate ET were scaled from single stems to stand level using allometry based LAI estimates. The good agreement with light interception derived LAI and the matching with literature data (e.g., Cernusca *et al.,* 1978; Johansson, 2000) makes us confident that we arrived at very realistic LAI. In forests, sapwood area or basal area is often used to calculate stand transpiration (e.g., Moore *et al.,* 2011, Gebauer *et al.,* 2012), yet, basal area does not necessarily scale proportionally to transpiration rates because of non-conducting heart wood (Moore *et al.,* 2011). Because *Alnus* has diffuse porous wood without a distinct sap- and heartwood differentiation (Schoch *et al.,* 2004), water can be expected to be

transported over the entire (ca. 2 cm) cross section of stems, especially, in such young stands. Since the stems used for sap flow measurements were similar in diameter to the mean stem diameter for the entire stand (transects), we do not expect a stem size bias in our scaling calculations.

High rates of transpiration in *Alnus* have been observed in other studies. Herbst et al. (1999) reported a higher seasonal transpiration in a stand of *Alnus glutinosa* compared to an adjacent beech stand, despite minor differences in LAI (4.8 m^2 m^{-2} in alder versus 4.5 m^2 m^{-2} in beech). The authors explained the higher transpiration by weak stomatal control and unlimited access to soil water, similar to what we observed in *Alnus viridis*. In comparison to literature values for other deciduous shrubs (g_{max} 270 ± 91, mean ± sd; Körner 1994), leaf conductance values for *Alnus viridis* we measured were very high indeed (maximum 404 ± 33 mmol m^{-2} s^{-1}, mean ± se). Even shaded leaves in dense stands showed high leaf conductances (195 ± 38 mmol m^{-2} s^{-1}).

Overall, this study adds a high mountain case to 'classical' paired catchment studies that have demonstrated higher ET rates for forested catchments in comparison to grassland (Bosch and Hewlett, 1982; Brown *et al.,* 2005; Farley *et al.,* 2005). Our results show that differences in ET between grass- and shrubland are particularly pronounced during days with high VPD. While grassland ET correlated strongly with available solar energy (canopy warming by solar radiation), a combination of high solar radiation and atmospheric forcing (VPD in particular) determine vapour losses from shrubland. This is in line with theory and experiments: a close correlation between solar radiation and ET for grassland has been observed by De Bruin and Stricker (2000). For forests, ET rates have been demonstrated to dependent much more on atmospheric forcing (Kelliher *et al.,* 1993).

We have scaled ET data from single rainless days to the entire growing season, and from plot scale to the upper Reuss catchment. These estimates suggest substantial

hydrological and economic consequences of *Alnus* expansion, but are likely to be conservative because *Alnus* retains its foliage longer into the late season, and thus, continues to transpire while grassland is already senescent. Differences in rainfall interception are hard to quantify especially for dense grasslands. In the Ursern valley it was found that for *Alnus* bushes interception losses amount to 24% of the incoming rainfall (long term average; LAI values were roughly 4.0 m^2 m^{-2}). Grassland interception losses were higher and equalled 30% of the incoming rainfall (LAI values were substantially lower and reached 2.0 m^2 m^{-2}; E. Lischer, unpublished MSc Thesis Univ. Basel). Dew formation was not explicitly accounted for. For grassland, dew formation is commonly limited (0.2 mm maximum, quantified for grassland lysimeters at a nearby site). Higher amounts have been reported for dwarf shrubs (de Jong *et al.,* 2002). Dew can be deposited from atmospheric moisture (dewfall) or it can come from condensating of water from within canopies (distillation). On moist soils under low stature plants, the latter is likely to be the dominant source, thus not adding significantly to the water balance.

The present study evidences that the replacement of extensively grazed montane grassland by shrubs enhances the evaporative water loss. Land abandonment thus, reduces hydrologically relevant ecosystem services. This comes in addition to other drawbacks such as reduced biodiversity, delayed or inhibited reforestation, lack of avalanche protection, higher risk for landslides (Tasser *et al.,* 2003, Caviezel *et al.,* 2014), increased nitrate leaching to soil and surface water, and enlarged N_2O emissions (Bühlmann *et al.,* 2014; 2016; Hiltbrunner *et al.,* 2014).

Acknowledgments

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Chapter 5: summary and conclusions

In this thesis I assessed the effects of land use and weather parameters on the water balance of ecosystems along a montane to alpine elevational gradient in the Swiss Alps (Ursern valley, Upper Reuss catchment). The measurement of evapotranspiration (ET) was central to my thesis. Commonly ET is estimated indirectly from concurrent measurements of catchment runoff and rainfall by solving the water balance equation. Such a catchment-wide approach includes signals from many different land surface types and is dominated by snow- and glacier-melt during the short alpine summer and thus, would not permit distilling subtle, vegetation-specific signals. In my thesis I therefore chose to determine ET directly. In the first paper (Chapter 2), I used a large number of weighable lysimeters (WL) fitted with grassland monoliths, evaporimeters (atmometers) and a physics based model (the Penman-Monteith model that calculates evapotranspiration for a reference grassland from weather parameters: PMET) positioned at a low (L), mid (M) and high (H) elevation site (1490, 1960 and 2440 m a.s.l.) to separate the elevational influences of weather (atmometers and PMET) and vegetation on ET for bright days. Additionally, I analysed the seasonal water balance by calculating ET from grassland monoliths in so-called deep seepage collectors (DSC). In a second study (Chapter 3), I explored the effects of land abandonment (grazing was simulated by a clipping treatment) on ET across the same elevational gradient using measurements from WLs to obtain ET for bright days and DSCs to determine ET for the whole season using water balance calculations. I collected bright day and whole season ET rates for a range of representative, clipped and non-clipped grassland types, for dwarf shrubs (at the two montane sites: L and M) and tall grass swards (H) that both represent later stages of abandonment. In a third project (Chapter 4), I quantified ET of *Alnus viridis,* (green alder) and compared it with ET of an adjacent montane grassland. This required the use of energy balance sap flow sensors mounted to *Alnus* stems. Understorey ET was measured with WLs. Stem-leaf allometry was used to scale from individual stems to the full canopy. The hypotheses tested within the scope of this thesis thus, all related ET to vegetation characteristics (biomass, LAI, that is, the leaf area index, and canopy height) and climatic forcing.

Since land abandonment increases leaf area, this should lead to higher ET rates and hence, reduce runoff while the hydro-electric potential of the catchment would be negatively affected. The ultimate aim of this work was to demonstrate how land use can influence the water balance in montane and alpine terrain.

Chapter 2: Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps

Does grassland ET, for single bright days as well as for the growing season (including bad weather conditions) change with elevation? If it does, is this because of a change in weather conditions, because of vegetation changes or both? For our test location in the Central Swiss Alps (where rainfall is commonly exceeding transpiration), *I expected that the micro-climatic effects compensate the reduced biomass and vegetation height, so that ET would not change with elevation (hypothesis 1).* The data obtained, however, unequivocally showed that weather and reduced biomass both cause bright day and longer-term ET to decline with elevation. This reduction in ET was due to both, reduced evaporative demand (data from atmometer evaporation and PMET) and reduced plant biomass (leaf area). Across the elevational gradient of approximately 1 km, atmometer evaporation declined by 23% and PMET decreased by 11%. Actual ET was reduced by 37%. Over longer sampling periods PMET decreased by 10%, while again the actual elevational reduction in ET was much larger and equalled 35%. For the lower part of the elevation gradient (L vs. M), the observed elevational decline in ET was mainly caused by climatology (similar decline in ET as in climatic forcing), while above that (M vs H), this decline was an outcome of both biomass and weather parameters (decrease in ET was by far larger than the decline in both atmometer evaporation and PMET). This can be explained by similar biomass at L and M, whereas biomass mainly decreased between M and H. The study hence concluded that the observed elevational decline was a result of a decline in both, atmospheric forcing and biomass, and hydrological models should explicitly account for both factors when modelling catchment ET (Van den Bergh *et al.,* 2013, Journal of Hydrology).

Chapter 3: Hydrological consequences of grassland abandonment along an elevational gradient in the Swiss Alps

In light of the results obtained in chapter 2, I then asked: what happens if montane or Alpine grasslands are abandoned and biomass (in essence LAI) increases? In order to find out, I simulated grazing by a standardized clipping of the vegetation (down to a stubble height of 3-4 cm that is common for sustainably grazed pastures). Comparing ET of clipped and unclipped vegetation allowed us to quantify the hydrological effects of continued land use and abandonment. Because vegetation biomass is normally higher at montane (L and M) compared to alpine (H) sites, *I expected the effect of abandonment on ET to be larger at L and M than at H (hypothesis 2)*. Higher ET as a result of land use cessation (taller grass) means reduced runoff and therefore also a reduction in watershed hydro-electric potential. I estimated the catchment wide consequences for discharge by scaling differences in ET between clipped and abandoned swards to the land area fractions represented by the three sites. By accounting for falling height (potential energy), I then calculated the hydro-electric value of continued land care for the Ursern valley (Upper Reuss catchment).

In line with hypothesis 2, the results show similar and large bright day abandonment effects at L and M for the three common grassland types (depending on the vegetation type up to 51%). At H, abandonment effects were commonly smaller (up to 8%) but vigorous, taller grassland types such as *Agrostis*, showed larger abandonment responses (up to 26%). In dwarf shrubs, we found ET rates between those of clipped and abandoned grassland, indicating that invasion of abandoned pastures by dwarf shrubs (mainly in the subalpine belt) could reduce effects of tall (abandoned) grass sward growth but still leads to higher ET compared to grazed land.

Long-term water balance data obtained from DSCs at first sight, seem to contradict these findings as significant water savings due to clipping were only found at the lowest site (runoff was reduced by a maximum of 66 mm after clipping until autumn). Experiments, by Inauen *et al.* (2013, Journal of Ecology) at H however, revealed that abandonment leads to significantly higher 'all weather' ET. Across a range of four different grassland types, abandonment increased 'post clipping' ET by 22 to 35 mm at H. For the tallest swards (*Agrostis*), ET increased by even 30 to 74 mm (runoff therefore decreased by this amount). The explanation for this apparent discrepancy between short and long-term results should likely be sought in the growing season weather conditions. Sampling periods of the experiments presented here were both obtained for comparably rainy summers while the large abandonment effects reported in the Inauen *et al.* study were found during a warm and comparatively dry season (summer 2009). Also, replication was higher in the Inauen study that was confined to H (but bucket volume was somewhat smaller: 10.5 v.s. 14.7 L). It thus seems that abandonment and the establishment of tall swards significantly enhances ET rates during summers with good weather conditions irrespective of elevation, whereas under more humid conditions, water savings due to grazing are primarily achieved in tall grass swards at lower, montane elevations (but effects are also small). Dwarf shrub invasion into abandoned grassland appears to reduce initial abandonment effects.

By using a digital elevation model and by assuming a producer price of electricity and an average efficiency of a hydro-power plant of 85%, I then calculated the reduction in the catchment's hydro-electric yield caused by land abandonment. *For lower montane areas (L) of the catchment, I expected that the potentially large increases in ET lead to small reductions in catchment hydro-electric yield due to the limited land area and height. High montane (M) and alpine lands (H) make up the largest part of the catchment. In addition, potentially smaller abandonment effects (in H) should become economically more significant also because of the greater falling height (hypothesis 3).* The results show that abandonment of all current grasslands at L would scale to costs of 0.1 to 0.4 Mio CHF per year. For M and H, these costs would scale, depending on weather, from 0 to 1.4 Mio CHF (M) and 0 to 1.2 Mio CHF per year (H). Per hectare,

land management produces revenues at L ranging from 33 to 135 CHF a^{-1}. For M, benefits can be much larger and vary between 0 to 235 and CHF ha^{-1}. At H we find revenues similar to those for the low belt, with the greater falling height not entirely compensating for smaller absolute abandonment effects: 0-125 CHF ha^{-1} a^{-1}. For the valley as a whole we calculate that land use benefits vary between 0.1 and 2.9 Mio CHF a^{-1}. The large variation results from the low effects during humid summers. As the climate continues to warm and summers tend to get longer and drier, the higher benefits of land use will become more likely.

Chapter 4 *Alnus* shrub expansion increases evapotranspiration in the Swiss Alps

Development of tall grass swards is however not the only consequence of abandonment. After several years of neglect, *Alnus* invades former pastures and meadows while it prevents further succession toward the original montane forest because of the species capacity to, symbiotically, fix di-nitrogen. The fourth chapter therefore, much like the third, aimed to quantify effects of *Alnus* encroachment on ET and the catchment hydro-electric potential. Generally, deforestation is known to increase catchment water yield while afforestation often has the opposite effect. *For the Alnus case, I therefore expected shrub establishment to enhance aerodynamic coupling and lowers canopy temperature. This means that VPD and wind should become more influential while a reduced surface temperature could reduce ET. Because of these counteracting effects, I expected similar ET rates for grass and green alder (hypothesis 4).* I investigated this question taking a physiological and climatological approach using again weighable lysimeters for a grassland plot and an adjacent *Alnus* bush where understorey ET was measured. *Alnus* (overstorey) ET was determined by employing energy balance sap flow sensors. I scaled these data to stand and catchment level.

The results show that shrub expansion leads to an increase in ecosystem ET of 31 ± 14% and consequently reduces catchment runoff. Across 11 bright days, average shrubland ET exceeded grassland ET by 1.2 mm d^{-1}. Grassland ET was more strongly depending on global radiation whereas ET rates in *Alnus*, as expected, reacted more strongly to VPD and wind. Across all sampling days, the shrub versus grassland differences were particularly pronounced for days with a high VPD. I used simple regression models to calculate grassland and green alder ET for the whole growing season. *Alnus* turned out to increase ET by about 80 mm per season (mid May – end September). For the Upper Reuss catchment (Ursern valley) this corresponds to a reduced hydro-electric potential of ca. 1.8 Mio CHF per year should all grassland up to the climatic treeline, become invaded by *Alnus*. Annual 'costs' of the terrain covered by Alnus in 2004/2005 (15.5 km^2) are in the order of 0.5 Mio CHF. Because we compared green alder ET rates to those from unclipped grass swards, effects resulting from *Alnus* colonisation, add to those initially observed after grassland abandonment as presented in the fourth chapter. These numbers do however, represent a maximum effect since not all grasslands will be transformed into shrubland and grazing pressure is never uniform across the entire catchment. Land use by farmers is thus not only instrumental in maintaining agricultural potential, biodiversity values and an attractive landscape, but it also serves to maintain highly tangible ecosystem services such as catchment water yield.

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Publications

Van den Bergh T 2017. *PhD thesis*. Hydrological consequences of grassland abandonment along an elevational gradient in the Swiss Alps. University of Basel. Switzerland

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The river Reuss at Zumdorf